# TAXONOMY OF THE GENUS *PERODICTICUS*

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TAXONOMY OF THE GENUS *PERODICTICUS*

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The specific and subspecific taxonomies of African primate populations such as *Cheirogaleus* and the Galagidae have been challenged in recent years (Bearder, Honess, Bayes, Ambrose, and Anderson 1995; Groves 2000), and it has been suggested that the taxonomy of another group, *Perodicticus*, may not adequately reflect the diversity of its members either (Schwartz and Beutel 1995; Grubb, Butynski, Oates, et al. 2003). Taxonomies are an organizational framework used by researchers conducting comparative studies, and their completeness and accuracy is important for evolution and systematics.

A representative sample (N=132) of specimens allocated to *Perodicticus*, representing the entire known geographic range of the genus, was examined and described by dentition, cranium, post-cranium, and pelage. Measurements were taken with sliding calipers, and tape and non-metric descriptions are supported by photographs. The descriptions (observed values) were then compared to summaries of distinguishing and diagnostic descriptive traits received from previous taxonomies (expected values).

Specimens were found that were highly congruent with traditional descriptions of the taxa *Perodicticus potto edwardsi*, *Perodicticus potto ibeanus*, and *Perodicticus potto potto*. A single specimen was found that matches the expected description for *Perodicticus potto faustus*, which is not taken as support for reviving that taxon out of its synonymy with *Perodicticus potto*

*edwardsi*. Specimens were found that partially resemble the descriptions for *Perodicticus potto ju-ju* and have been tentatively identified as such. Previously undescribed features present in the population assigned to the genus *Perodicticus* have also been found, including a bowed fin on the mesial margin of the lower (caniniform) anterior premolar in most of the specimens conforming to the descriptions for *P. p. ju-ju* and *P. p. potto*.

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## PREFACE

This project grew out of my desire to understand how theory and practice are interconnected in evolutionary biology and the systematics of evolution. The practice of taxonomy is an act of creation in which a set of objects are recognized and set apart by some criteria through the process of naming. The taxon becomes an object itself, and the taxonomy, the organization of the world through named groups, reflects the assumptions and biases (physical, experiential, methodological, and theoretical). It is taxonomy that generates and is generated by the hypotheses of comparative studies.

In particular I have been interested in the species problem. Species are defined by some criterion or suite of criteria that is supposed to characterize a biological population, and those processes which produce populations conforming to these criteria are then dubbed speciation. The opposite process, defining species through process, is as far as I know represented only by those invoking Special Creation. The species problem arises, then, as a particular process may not always have the same outcome. That is, sometimes a process may produce populations which fit a particular set of criteria for a species, but other times it may not. Then there is the fact that multiple processes may produce similar or identical outcomes. Finally, there is general disagreement about what criteria to use—phenotypic distinctiveness (which aspect—morphology? behavior? physiology?; what properties—uniqueness? magnitude?) or reproductive distinctiveness (extrinsic or intrinsic? provoked by biological or non-biological factors? permanent or temporary?). Or some combination of the two?

While quite interesting debate continues over the species problem itself (even how to define the problem!), the two outcomes, phenotypic distinctiveness and reproductive distinctiveness, along with the processes producing them, continue to be important topics in spite of whether a particular view of speciation waxes or wanes. To properly address this problem to and to facilitate the comparative study essential to evolutionary biology, both phenotypic and reproductive distinctiveness need to be accurately described and reported. Taxonomic assignments may be based on either or both of these criteria as seen fit by practicing taxonomists, whether or not the specimens allocated to one taxa have the same relationship to each other as specimens allocated to another taxa of similar rank. Hence it is important to evaluate how taxa are defined and whether these definitions are justified. The current study addresses these very questions for the taxon known as *Perodicticus*. It is a step towards sorting through the layers of assumption that have accreted to many of the lesser studied primate populations, and ultimate to questioning the very sources of those interpretations. Anyone doing a comparative morphological study including the potto should be aware of the phenotypic differences that are and are not reflected by various taxonomies of the group.

I would like to thank the many people and institutions that helped make this study possible. My academic advisor and the chair of my dissertation committee, Dr. Jeffrey Schwartz, not only taught me extensively about morphology, systematics, evolution, and taxonomy, but he constantly required that I inspect and evaluate even the most obvious sounding propositions I made in my writing ("So what is a potto, anyway?"). Dr. Michael Siegel provided very valuable advice concerning the presentation of ideas in general and grant-writing in particular. He and Dr. Mark Mooney also made very valuable comments regarding the statistical analysis of the

morphometric data presented in this study and along with Dr. Schwartz provided a great deal of encouragement at all phases of the completion of this project. Dr. Bryan Hanks and Dr. John Wible presented not only many helpful corrections and suggestions for improving this document but also ideas for future publication.

In addition to his role as a member of the doctoral committee, Dr. Wible was also the curator of one of the collections examined in this study. Along with Susan McClaren and the staff of the Section of Mammals at the Carnegie Museum of Natural History in Pittsburgh, he provided generous access not only to primate skins and skulls but to photographic and computer equipment and microscopes as well. Similarly Linda Gordon, the Collections Manager for the Division of Mammals at the Smithsonian Institution in Washington D.C., provided access to the primate range of specimens, helpful equipment, and to a quiet room in which to work. The same helpfulness and accommodation was also provided by Jean Spence, Teresa Pacheco, and the staff at the American Museum of Natural History in New York.

The faculty and staff of the Department of Anthropology have been a continuing source of support during the process of completing this project and the degree for which it is requirement. Phyllis Deasy, the Graduate Secretary, Kathy Allen, the departmental secretary, and Felice Kappel and Donna Yurko, Department Administrators, were essential to helping me keep up with all of the required paperwork and also provided encouragement.

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# 1. INTRODUCTION

## 1.1. Nature and Scope of Issue

Taxonomic decisions have a direct impact on the kinds of systematic hypotheses generated as well as the possible evolutionary explanations about a particular taxon or set of closely related taxa. Comparative taxonomic studies are essential to generating and testing hypotheses regarding evolution, which makes reliable taxonomy essential to generating and testing and such hypotheses. When the quantity or quality of differences within a group make such proxy inadvisable, the taxon must either be merged with a larger taxon or be broken down into more appropriate units. Moreover, since different types of research questions may require different ways of dividing the taxa and since multiple observers may emphasize different traits, inconsistent or competing taxonomies may emerge. In addition, misidentification or mislabeling of taxa may also occur. The re-evaluation of traditional taxonomies can help to identify and rectify these problems.

An opportunity to examine the effects of taxonomic decisions and contribute to empirical taxonomic research through the re-evaluation of traditional taxonomies was identified within the lorisiform primates. Among the small nocturnal African mammals are primates such as those classified as *Cheirogaleus*, *Perodicticus*, and *Galago*. These groups were revised in the early 1930s to reflect less taxic diversity than previously described (Schwarz 1931a, 1931b). In the

latter half of the twentieth century the galagos went from a single genus and half a dozen species to four genera and close to 20 species (Bearder et al. 1996). Many morphological and genetic studies of species and subspecies of the galagos have been undertaken in the past decade (for example see Anderson 2000 or Masters and Bragg 2000) in light of theoretical and methodological changes (i.e. the mate recognition concept of species (Paterson 1985) which have suggested cryptic speciation among this group of nocturnal primates. In addition, Groves (2000) has re-examined the genus *Cheirogaleus* and discovered unrecognized diversity among the dwarf lemurs.

Meanwhile, the pottos are still largely viewed as a single, moderately polytypic species occupying a single genus, *Perodicticus*. A new genus has been based on specimens previously attributed to potto (Schwartz 1996), and a preliminary analysis by the same researcher has suggested that additional undocumented differences may be present within the taxon (Schwartz and Beutel 1995). Despite a good deal of published data on the anatomy and received taxonomy of the potto, there is a dearth of literature challenging, revising, or documenting novel taxonomic descriptions.

The recognition and hierarchical ranking of taxa comes from the experience and judgment of professional taxonomists. The resulting taxonomies are subject to prevailing theories of the nature of taxa, including definitions of the units of taxonomy and models for the origin of the features used to recognize taxa. In some taxonomies the criteria for identifying and naming new taxa are absent or unclear, or, given changes in the theory and method for identifying taxa or the discovery of new specimens, the reasons previously given for creating and naming a separate

group may not be as convincing as they once were. Given the importance in systematics of comparing interspecific and intraspecific differences, the reliability of the taxonomies used is critical. The re-evaluation of traditional taxonomies, then, is a valuable exercise that strengthens the research that rests upon taxonomic accuracy.

This study sampled morphological data (features of the pelage, cranium, post-cranium, and dentition) from the currently known range of the genus *Perodicticus* to test the traditional taxonomy and to address whether unrecognized, forgotten, or neglected taxic potential can be found in pottos.

## 1.2. Introduction to the Genus *Perodicticus*

The common name for the animals attributed to the genus *Perodicticus* is potto. The potto is generically described as a slow-climbing nocturnal omnivore that occupies an area that stretches from Liberia and Sierra Leone in the west of Africa to Kenya and Uganda (Fleagle 1999). Pottos tend to be the size of small to large domesticated cats. Like other lorisids they have a reduced second manual digit and laterally oriented tubular expansion of the petrosal region (Schwartz and Tattersall 1985). The teeth of the potto are very low and rounded.

Among the earliest recorded citings of pottos is the report by a Dutch sailor named van Bosman in 1699. Specimens attributed to the group were placed in the genus *Nyticebus* in 1812 and 19 years later this taxon assigned to its own genus, *Perodicticus*, by Bennet (1831), who described the new taxon thus: "By the comparative length of the tail…in the moderate elongation of the

face, in the moderate size of the ears, in the equality of the limbs, and especially in the extreme shortness of the index of the anterior hands, reside its essential features" (110). The pelage is a "chestnut mixture with a light shade of grey" (110), and Bennet also notes from the observations of a fellow naturalist that they tend to come out at night and feed primarily on vegetation and act in a "slothful and retiring" manner.

The genus *Perodicticus* would eventually hold several different species, many named by Oldfield Thomas. Thomas (1910a) described his view of the genus very succinctly: "The Pottos fall readily into two groups, large-toothed and small-toothed. The former are *P. edwardsi* and *batsei*, the latter *P. potto*, *ibeanus*, and the present form ["*ju-ju*"]." He further subdivided the large and small-toothed pottos by their pelage and locality.

The genus was reduced to a single species, *Perodicticus potto*, by Schwarz (1931) that contained four subspecies (*potto*, *edwardsi*, *faustus*, and *ibeanus*). As a justification for this change, Schwarz cited his concern that many differences used to identify species of potto, primarily size and colour differences, reflected either different ontogenetic phases of the same animal or the normal range of variation found in mammalian species. In his work on the anatomy and taxonomy of primates, Osman Hill (1953) affirmed this view, stating that "the animal is subject to great individual variation in colour, as well as size, and this has lead to the unnecessary multiplication of named forms" (190).

Hill, however, retained *P. potto ju-ju* as a viable taxon, and summarized the locality, pelage, and distinguishing craniodental features associated with each subspecies. Hill lists *P. potto potto* as

the smallest taxon, with reddish-brown fur and a dark spinal stripe that fades posteriorly. Dentally "the foremost lower premolar [likely the middle lower premolar in current nomenclature as this was identity of the shape/position in which such a tooth was found in this study] is noticeably smaller than its successors. This applies to some extent to the corresponding upper tooth" (1953: 192). Hill adopted the description of *P. potto ju-ju* as the grey colored member of the small-toothed pottos and lists them as occupying southern Nigeria, forming the eastern border of the range for *P. potto potto*. *P. potto edwardsi* was described as the largest form with very large cheek teeth, deeper hues of brown and red, strongly developed bristles, and silvery colored juveniles. The range of *edwardsi* was listed as Cameroon and Gabon. *P. potto faustus* is described as having cinnamon colored fur with dark hairs interspersed, a smaller skull, but larger cheek teeth, living west and south of the Congo River. North of *faustus* and east of *edwardsi* is *P. potto ibeanus*, with a brownish head, dark shoulders, and ashy posterior.

The three taxa most likely to be recognized in contemporary taxonomies include *P. potto potto*, *P. potto edwardsi*, and *P. potto ibeanus*, though *P. potto ju-ju* and *P. potto faustus* still often receive a passing reference (Kingdon 1997). Schwartz and Beutel (1995) have suggested that there are two basic craniodental morphotypes within the genus *Perodicticus*, labeled as "textbook" (or the common potto description) and "Zürich". Within the Zürich morph they proposed two strong subtypes and a few other potential morphs. Schwartz (1996) then proposed that primitive retentions such as the presence of an entepicondylar foramen on the humerus and a significantly longer tail as well as features such as a reduced upper middle premolar and a tiny $M^3$ were sufficient to distinguish a new taxon, *Pseudotto martini*, from the potto population.

While there has been debate and speculation about the validity of *Pseudopotto* (Groves 1998; Sarmiento 1998), there is a common sentiment that the traditional taxonomy of those primates represented by the single genus and species *Perodicticus potto* may be insufficient:

> "We recognize one species of potto for the time being, but acknowledge that further study may show that there are several valid species in the genus. The populations currently grouped in *Perodicticus potto edwardsi* probably comprise several taxa"
> (Grubb, P., Butynski, T., Oates, J. et al. 2003: 1323).

The results of this study are relevant to pursuing such concerns by testing the traditional taxonomy for the subspecies of *Perodicticus* and contributing novel observations of differences in the genus.

### 1.3. Taxonomic Analysis

The current taxonomic system employs the binomial nomenclature established by Linnaeus, which includes the genus name and the species name. In addition a third term, designating the rank of subspecies, may also be used. The identification of taxa and their subsequent ranking in the Linnaean hierarchy is a long-standing source of disagreement. Testing the traditional taxonomies of *Perodicticus* requires an appreciation of the relevant issues surrounding the recognition, naming, and ranking of taxa.

It has been suggested that distinction between groups is most readily seen at the level of the genus than the species (Simpson 1944). Thus while species names may be duplicated, the genus is supposed to be the pivotal level of taxonomic distinction and so a genus name must be singular. A small sample of species concepts serves to illustrate the commonalities and differences in the use of the term species in evolutionary biology.

By advocating the idea that one species is formed gradually from another species through descent with modification, Charles Darwin's work suggested that the differences between an incipient species and a fully realized species were only fully realized through the loss of intermediate forms linking them together, while the characters used to identify species could be the same as those marking incipient species (Darwin 1859:485):

"Hereafter we shall be compelled to acknowledge that the only distinction between species and well-marked varieties is, that the latter are known, or believed, to be connected at present day by intermediate gradations, whereas species were formerly thus connected."

Adopting Darwin's focus on populations, Mayr (1942:120) proposed that most animal species could be defined as follows:

"Groups of actually (or potentially) interbreeding natural populations which are reproductively isolated from other such groups."

Although the Biological Species Concept is not the only available definition, it is still appears to be the most widely used definition. Additional species definitions have been suggested since the BCS and many still have active advocates.

The paleontologist G.G. Simpson (1961) proposed the **Evolutionary Species Concept** (ESC):

"An evolutionary species is a lineage (an ancestor-dependent sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies."

An immediate concern is how to define "role" and "tendencies." The former may suggest an ecological or adaptive specialization, while the latter demonstrates a focus on the fossil record (since "tendency" in an extant population requires the researcher to know what will happen to the species in the future).

Alan Templeton (1989) proposed the **Cohesion Species Concept**:

"The most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms"

Templeton suggests that phenotypic cohesion is not necessarily maintained by reproductive criteria [genetic and demographic "exchangeability" are emphasized].

The **Phylogenetic Species Concept** was introduced by Joel Cracraft (1983):

"The smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent."

Cracraft emphasizes a diagnostic feature (autapomorphy) as being essential, yet claims that such features may not always be morphological and in some cases may only occur in a single sex or in a particular developmental stage. Reproductive isolation may be presumed, but its demonstration is not required, which allows for the inclusion of fossil taxa.

Hugh Paterson (1985) offered the (**Mate) Recognition Species Concept:**

"That most inclusive population of biparental organisms that share a common fertilization system."

The subtlety of the definition is that it does not specify exactly how mates recognize one another—visually, chemically, physically, ethologically, etc.—but it does imply that specific mate recognition systems produce real, discrete groups. It is similar to the definition offered by Plate (1914, cited in Mayr 1957): "The members of a species are tied together by the fact that *they recognize each other as belonging together* and reproduced only with each other" (Mayr 1957:8).

While highlighting only a few of the more popular species concepts, the preceding list demonstrates two important elements of creating a species taxon—*phenotypic distinction* and

*reproductive isolation*. Additional elements include geographic dispersal of the individuals in each presumptive taxon and a shared presumed ecological role or niche of those individuals. Phenotype in this instance may refer to any readily observable macroscopic traits of the organisms in question including both soft and hard morphology as well as behavior.

As for subspecies, Mayr wrote: "A subspecies is an aggregate of phenotypically similar populations of a species inhabiting a geographic subdivision of the range of the species and differing taxonomically from other populations of the species" (Mayr 1970: 210). He clarifies that to differ taxonomically means to differ by diagnostic morphological characters, but the necessary degree of difference for recognizing subspecies was left to agreement among working taxonomists. For the traditional taxonomies of *Perodicticus* it appears that criteria similar to what Mayr articulates regarding subspecies was employed, although normally the taxonomies did not formally address the issue of the definitions of species or subspecies employed in naming and ranking the taxa.

A term that is sometimes used by taxonomists and systematists is "morph". It may or may not be equivalent to the older taxonomic term "variety" or the term "phenon". A morph is a group of specimens which differ from similar specimens by diagnostic morphological characters. According to Mayr then a morph is a subspecies if it is geographically distinct and *not* reproductively isolated from closely related specimens, and it is a species if such geographically isolated morphs *are* reproductively isolated. If reproductive isolation occurs between isomorphic groups, the two populations are referred to as sibling species.

Whether or not one uses Mayr's particular definitions for species or subspecies, they do reflect the concern over identifying morphs and questioning their reproductive compatibility as artifacts of the processes of evolution. The identification of morphs, then, is a basic element of recognizing, justifying, and therefore of testing taxa.

This study is based on the following premises:

1) historical groups (lineages) that are also phenotypically similar groups or reproductively compatible groups can be identified in nature;

2) the smallest identifiable groups tend to be incorporated into taxonomies as demes, subspecies, or species depending on the operational definitions of these terms used by the taxonomist;

3) properly identifying and sorting phenotypic, genetic, and reproductive evidence for morphs to justify taxa, regardless of the provisional rank assigned, is essential to both proper taxonomy and therefore to many basic evolutionary hypotheses.

### 1.4. The Hypotheses

The general hypothesis for this study rests on the presumption that the previously recognized subspecies are based on reliably identifiable morphs. That is, they possess features or suites of features by which they may be readily identified and distinguished.

The primary hypotheses are:

**"The taxa previously recognized as species and later demoted to subspecies within the group *Perodicticus* constitute robust morphs, that is, they are phenotypically well-distinguished from other specimens attributed to the genus *Perodicticus*."**

**"There are no morphs which can be identified within the specimens attributed to *Perodicticus* which would lump or split the currently recognized subspecies."**

Observations previously made which are relevant to testing these hypotheses include the mention of an unusually small premolar in the *P.p. potto* subspecies (Hill 1953) and two basic dental morphotypes highlighted by the arrangement on the upper canine-premolar series either being a stepwise reduction in size or demonstrating a marked size difference between the canine and the premolar series (a difference not attributed to a subspecies or geographic range; Schwartz and Beutel 1995).

The hypotheses suggest the following predictions:

- There will be no unrecognized/mischaracterized novelties in the dentition
- There will be no unrecognized/mischaracterized novelties in the cranium
- There will be no unrecognized/mischaracterized novelties in the post-cranium

- There will be no unrecognized/mischaracterized novelties in the pelage

## 1.5. The Principal Results

The population commonly referred to by the taxonomic nomenclature *Perodicticus* does exhibit both regional and non-regional recurring differences. Among those differences previously ascribed to the genus in taxonomic literature which have been confirmed by this study are:

- pelage differences, in particular between two forms of the western portion of the population (which is the primary basis for distinguishing populations which may validate the taxa *P. p. potto* and *P. p. ju-ju*), the central portion of the population, and the eastern portion of the population;

- differences in skull and molar size, again reflecting regional differences with some intra-regional distinctions;

- differences in the relative sizes of the upper canine and premolars as either step-wise or drastic in series;

- presence of an especially small lower (and at times corresponding upper) premolar in the eastern distribution of the population.

In addition new or previously unrecognized traits were also revealed:

- the presence of a strongly bowed "fin" on the lower anterior ("caniniform") premolar distributed in the eastern region of the population's range, is described in this study.

- a very noticeable difference between some regions in the length of the tail, from midway down the leg to well onto or past the hind feet.

- alternate pelage colorations/patterns, including a medio-lateral shift from light to dark hues and a rippled appearance in some specimens.

An analysis of these morphological findings suggests the following regarding the taxa under scrutiny:

- Specimens with frequently reddish fur and the largest molars and cranial lengths in the sample from the central region of the range of *Perodicticus* conform to the previously established expectations for ***P. p. edwardsi***; however, other pelage colors are present from this range with similarly large skulls and cheek teeth.
- Only one specimen in the study had all of the features shared with *P. p. edwardsi* and ***P. p. faustus*** (large cheek teeth, reddish fur) as well as the listed trait distinguishing *P. p. faustus*, a noticeable smaller skull.
- Specimens from the eastern range of *Perodicticus* with large, long bodies and a distinctive tri-colored pelage (in particular a dark zone across the shoulders/nuchal

region) were found which conform to the previous descriptions of ***P. p. ibeanus***; however, they did not possess the relatively long tails originally described for the taxon.

- Specimens from the west-central to the central-western region of the range of *Perodicticus* with grayish pelages were identified, which correspond to descriptions of ***P. p. ju-ju***. However, their skulls were not appreciably larger than the specimens corresponding to *P. p. potto* as per the description of *P. p. ju-ju*, and their tails tended to be shorter than *P. p. potto* as well, also contradicting the description of *P. p. ju-ju*. Moreover, specimens usually possessed a previously undescribed feature, a swelling of the mesial keel of the lower caniniform anterior premolar into a bowed fin, a feature shared with specimens matching the descriptions for the taxon *P. p. potto*.
- Specimens from the western range of *Perodicticus* with brown coats, a dark dorsal stripe, tiny upper (and sometimes lower) middle premolars, and relatively small skulls and teeth were found, matching the description of ***P. p. potto***. However, the small middle premolar was confined to the central portion of the range of *P. p. potto*. Also, specimens from this region had the longest tails for the genus. As noted for *P. p. ju-ju*, the possession of a bowed-fin on the mesial aspect of the lower anterior (caniniform) premolar is common in specimens otherwise matching the description for *P. p. potto*.

# 2. METHODS AND MATERIALS

## 2.1. Abbreviations

The following abbreviations were used in various texts and tables:

- **USNM** = United States National Museum, Smithsonian Collection
- **AMNH** = American Museum of Natural History
- **CM** = Carnegie Museum of Natural History
- ***P. p.*** = *Perodicticus potto*
- **Ssp.** = subspecies
- **ulm** = upper left molar, hence ulm1 is upper left first molar and ulm1leng is upper left first molar length
- **urm** = upper right molar
- **llm** = lower left molar
- **lrm** = lower right molar
- **aum** = average upper molar
- **alm** = average lower molar
- **maxleng** = maximum cranial length
- **maxwid** = maxium cranial length
- **nasal** = maximum length of the nasal bones

- **mintemp** = minimal distance between the left and right temporal lines

## 2.2. Sample

A total of 278 prosimian specimens were examined.

For this study 132 primary specimens attributed to the genus *Perodicticus* housed at the United States National Museum—Smithsonian Institution (NMNH), the American Museum of Natural History (AMNH), and the Carnegie Museum of Natural History (CM) were examined to confirm and identify morphological differences in the taxon. This sample includes specimens from the entire known range of the taxon.

The data collected for each specimen of this taxon when available include the museum and collection number under which it is housed, the sex, the country and locality in which the specimen was collected, and the nomenclature listed on the specimen label. Dental age (deciduous, permanent, or mixed) was irrelevant because of the paucity of available specimens from the different regions of interest with less than full permanent dentition. All specimens in the study either possess full permanent dentition or their stage of dental eruption is sufficiently advanced to properly diagnose features from the permanent teeth (i.e. the one or two remaining deciduous teeth simply have yet to shed and the permanent tooth is almost completely erupted). The only exceptions were specimens with both pelage and skull present in which the size of the skull, completely deciduous dentition, and small body size (as suggested by the pelage) indicated

an infant or very young juvenile. Only comparative descriptions of pelage coloration were included from such specimens.

In addition to the specimens attributed to *Perodicticus*, specimens labeled as belonging to the following genera were also described: *Loris* (3 specimens from the NMNH), *Nycticebus* (54 specimens from the NMNH), *Arctocebus* (3 specimens from the NMNH), and *Galago* (82 specimens from the NMNH). The descriptions for these specimens included notation of general size and body proportions, pelage coloration and patterns, notable cranial features, and dental descriptions.

### 2.3. Data Collection

For the specimens of *Perodicticus*, the measurements were chosen based on traditonal taxonomies for the genus (Thomas 1910a, Thomas 1910b; Schwartz and Beutel 1995) and the general conditions of the specimens, allowing for a test of previous characterizations of *Perodicticus* populations based on metric data and an investigation of the relationship of metric data to previously and newly recognized non-metric traits characterizing these populations. Measurements included: maximum skull length, maximum skull width, maximum length of the nasal bones, minimum separation of the temporal lines, maximum length and width of upper and lower $1^{st}$ and $2^{nd}$ molars, maximum humeral length, and maximum femoral length. Measurements were selected based on the metric traits most commonly examined in previous studies to facilitate the evaluation of those studies. All measurements (in cm) were taken with a Helios manual sliding calipers except for pelage and tail length, which were measured with a

measuring tape. Measurements were repeated twice in order to reduce intra-observer error. The average values were entered into SPSS 11.5 for statistical treatment.

Descriptions included features that were suggested as taxonomic indicators within *Perodicticus*, such as pelage coloration, or which were suggested as distinguishing characteristics of the genus *Pseudopotto*: a tiny triangular upper middle premolar, the presence or absence of a bifid spinous process for the second cervical vertebrae, and the presence or absence of an entepicondylar foramen on the humerus. Novel non-metric features, including recurrent and individual dental variations, were also included.

Categorical variables such as the presence or absence of a bowed fin on the lower caniniform 1$^{st}$ premolar, the presence or absence of a bifid spinous process on the second cervical vertebrae, the presence or absence of an entepicondylar foramen on either humerus (left and right), the sex of the specimen, the country and locality in which the specimen was collected, and the taxonomic allocation listed on the specimen label were also entered into SPSS 11.5 for statistical treatment. Photographs of the dentition were taken with a Nikon (D1) 5012257 camera with a 150 mm AF Micro lens. Pictures of potto pelages were originally shot with a Sony Digital 8 HandyCam (DCR-340), captured with Studio 8 software on a personal computer, and edited (cropped and resized) with Paint Shop Pro version 7.

The specimens taxonomically allocated to *Arctocebus*, *Nycticebus*, *Loris*, and *Galago* were treated in a similar fashion, but no measurements were taken. The full listing of data pertaining to both potto and non-potto specimens is included in the Appendices.

## 2.4. Novel Descriptive Terms

There is a novel description employed in this study for a common shape encountered in the upper premolars referred to as "arrowhead". This description is based on a lingual view of the tooth, in which the mesial and distal slopes of the paracone rise sharply to meet at the tip and both slopes are equal in length. This produces a squat triangular shape. In addition, small stylids on the lower ends of the slopes serve to give the impression of a spear head or arrow head, and hence the term.

## 2.5. Assumptions and Biases

One potential source of bias is the *sampling method*. At the level of collecting and processing specimens, this potential bias is always present when utilizing museum collections. One remedy employed in this study is to use multiple collections which contain specimens from the entire known range of the taxon in question. The *Perodicticus* sample includes multiple specimens from Liberia, Ivory Coast, Ghana, and Benin in the western range of *Perodicticus;* Nigeria, Cameroon, Gabon, the Central African Republic, and the Democratic Republic of the Congo (formerly Zaire) in the central range of *Perodicticus*; and Uganda and Kenya in the eastern range of *Perodicticus*. Another is to check for discrepancy by age or sex. The overwhelming majority of the skeletal specimens are dentally adult (full permanent dentition). That sample is 39% female (n=51), 52% male (n=69) and 9% (n=12) indeterminate.

Another potential source bias is *sample size*. There is a danger in smaller sample sizes of over-estimating differences between two sets of specimens, while with larger sample sizes there is an increasing tendency for statistical tests to report weak correlations as having a high degree of significance. There is a difference, though, between significance (in statistical terms) and meaning. Since the study was intended to identify readily recognizable differences at any population level or within any subgroup of the genus *Perodicticus*, any novel descriptions are meaningful. Also, since there is less chance of establishing high levels of statistical significance from comparing smaller samples, any notably values of significance linking two or more variables provide hypotheses for retesting with larger sample sizes. While it is certain that undescribed features will have a greater chance of discovery, as part of a phenotypically cohesive subunit within the genus *Perodicticus,* they should be apparent by examining a sufficient geographic range.

# 3. TRADITIONAL TAXONOMIES OF *PERODICTICUS*

## 3.1. *Perodicticus*—Recognizing a Potto

The following subsection gives some comparative information about how pottos are similar and dissimilar from taxa which are generally regarded as being closely related to the genus *Perodicticus*. The summaries provide distinguishing features which help to validate *Perodicticus* as a valid taxon. This is followed by sections giving descriptions for the taxa within *Perodicticus*.

### 3.1.1. Dentition

To appreciate the context of the detailed descriptions of the specimens of *Perodicticus* provided, a general overview of the features found in other similar taxa is provided, including specimens from *Loris*, *Nycticebus*, *Arctocebus*, and *Galago*, based on observations made in this study.

In the *Loris* specimens, both $I^1$ and $I^2$ are skinny and peg-like. The upper canine is taller than the other teeth and bladelike with tall slender keels, and the upper $P^2$ is two thirds the height of C with flared mesial and distal stylids. There is a mesiolingual swelling (protocone-like) on $P^3$ and a smaller one added mesiodistally (hypocone-like) on $P^4$. $P^2$ is only slightly taller than $P^3$ and $P^4$. $M^1$ is similar to $P^4$ except the former possesses a second clearly defined metacone. On the upper

molars is a shallow basin formed by the pre- and post-protocristae, and a small notch isolates the hypocone. The cusps of the molars are tall compared to *Nycticebus* and *Perodicticus* and fairly pointed. $M^2$ is a little bigger than $M^1$, while $M^3$ is a little smaller than $M^1$.

The toothcomb in *Loris* has four smaller compressed central teeth and two larger lateral teeth. $P_2$ is taller than the other teeth with keels and the distal keel falls away into a small plateau. $P_3$ has a slanted keel-like cusp-like protoconid surface forming a small ledge running down and distal on the lingual side to join a narrow plateau on the distal end of the tooth. $P_4$ has a similar paracone that is more obviously triangle-shaped as well as the same distal plateau. All three lower molars have a clearly visible paraconid shelf on the mesial margin. The protoconid and metaconid are very tall, almost twice as tall as the other cusps, and fairly pointed with a cristid obliqua running from the hypoconid to the lingual base of the protoconid where a crest connects the protoconid and metaconid. The hypoconid is taller than the entoconid. The talonid basin is very deep. A hypoconulid is present on the third molar and is the same size as the other distal cusps.

In the *Nycticebus* specimens the $I^1$ teeth are bigger and flatter than those observed in *Loris*, while the $I^2$ are smaller and rounder and more peg-like. The upper canine is taller than the other teeth, thick, and curved with slender keels. The $P^2$ has an arrowhead shape and is half the size of C and twice the size of $P^3$ and $P^4$. $P^3$ and $P^4$ are smaller arrowhead shaped paracones with lingual plateaus and protocones only hinted at in their slightly raised lingual margins. The upper molars have a fairly wide notch separating the hypocone from the main trigon. $M^1$ is a little bigger than $M^2$, and $M^2$ is a little bigger than $M^3$. The cusps are not as tall and sharp as those found in *Loris*.

The toothcomb in *Nycticebus* has four smaller and more slender central teeth and two larger keeled lateral teeth. $P_2$ is tall and curved with a strong mesial keel that bows out a little. $P_3$ and $P_4$ have single triangular protoconids with a small disto-lingual plateau fed by a slight short lingual cingulum ledge. The lower molars have a shelf on the mesial margin, the protoconid and metaconid are twice as tall as the hypoconid and entoconid (and hypoconulid), and the talonid basin tends to be more deeply excavated between the metaconid and entoconid. The buccal margin is a wall created by the cristid obliqua coursing to the crest between the protoconid and metaconid toward the base of the protoconid. A small hypoconulid is often seen on $M_3$. $M_1$ is slightly larger than $M_2$, which is slightly larger than $M_3$. The main distinction observed within *Nycticebus* is that *N. c. borneanus* and *N. c. javanicus* only have central upper incisors (at least in the adults).

In the *Arctocebus* specimens both the central and lateral upper incisors are of the smaller, spindlier variety. The upper canine is stout and fairly straight and steps down by height by half from $\underline{C}$ to $P^2$ to $P^3/P^4$. $P^4$ and the upper molars are squared by and extremely strong band of cingula which encircle those teeth. The cusps on the premolars and molars are very tall and very pointed, and the crests, such as the pre- and post-protocristae on the molars, are very strong and tall. $M^2$ is a little bigger than $M^1$, which is a littler bigger than $M^3$.

The six-toothed tooth comb of *Arctocebus* resembles that of the previously described lorisiforms, with 4 compressed or more slender central teeth and two larger keeled lateral teeth. $P_2$ is tall and canine-like as above. It has a deeply grooved mesial keel. Both $P_3$ and $P_4$ are single cusped

teeth (protoconids) with a deeply grooved and bowed mesial keel that sweeps back on the lingual surface as a ledge. The molars are fairly similar in size, with very tall protoconids and metaconids, a deep talonid, and a cristid obliqua running along the buccal margin from hypoconid to the region at the base of the protoconid where it receives the short crest from the metaconid.

In the *Perodicticus* specimens, although the central incisors are a little larger than the laterals, the laterals look like they have the same basic configuration, the shape of the central upper incisors of *Nycticebus*, just as the central and lateral incisors of *Arctocebus* and *Loris* resemble the spindly lateral incisors of *Nycticebus*. The upper canine is large and curved and may be described as dagger-like. The $P^2$ is generally a smaller version of C, and $P^3$ and $P^4$ have a single-cusp (paracone) with the outline of an arrowhead. There is no lingual bulge or ledge on $P^3$ suggestive of an aborted protocone as per the previous genera. The molars have a moderate notch separating the hypocone from the trigon and moderate-to-weakly developed pre- and post-protocristae. The premolar and molar cusps are very low and rounded and tend very much to resemble those of *Nycticebus*. There is also a tendency in *Perodicticus* to develop miniscule $M^3$s which are half the size or less of the other upper molars, and this seems to be unique to pottos among lorisiforms. Differences between subspecies of potto will be discussed shortly.

The tooth comb in *Perodicticus*, as with the other lorisiforms, has four slender central teeth bounded by two larger compressed and keeled teeth. The $P_2$ is also typical for lorisiforms as it is tall and caniniform. Some potto populations, however, possess unique ornamentation to these teeth to be described in the following sections. The $P_3$ and $P_4$ are single-cusped teeth

(protoconids) with a somewhat triangular shape and a short distal ledge. The lower molars have very tall mesial protoconids and metaconids, although they are lower and rounder than the previous genera. The metaconids and entoconids sometimes appear somewhat compressed and squashed into the lingual margin. A brief cristid obliqua drifts from a more central course toward the meeting of the protoconid and metaconid to a course toward the metaconid.

In *G. crassicaudatus lonnbergi* the $I^1$ and $I^2$ are the same size but they are smaller and shorter than those of *Perodicticus* (but not yet spindly). The upper canine is large with a blip of a mesial stylid and a small distal stylid. $P^2$ is one third the height of C and a bit taller than $P^3$. $P^2$ has a single tall, flat sharp paracone with a blip of a mesial and a distal stylid that swing out and away from the cusp. $P^3$ is a mini-version of $P^2$ and somewhat taller than $P^4$. $P^4$ is completely molariform, where the hypocone is a ledge on a rounded disto-lingual corner that steps down from the edge of the post-protocrista. The molars resemble the $P^4$, and the size is graded by downward steps as follow: $M^1 – M^2 – P^4 - M^3$.

The toothcomb in *G. c. lonnbergi* has four smaller central teeth and two larger lateral teeth. $P_2$ is caniniform, tall, slender, and curved but slender with a well-developed mesial keel. $P_3$ has a broad/flat distal occlusal surface which narrows as it rises mesially to the point of the protoconid. On the lingual side of the top of the tooth a diagonal fold appears, running from the point of the protoconid to the lingual margin and producing another facet on the lingual side. This facet is bounded superiorly by the point of the protoconid and anteriorly by a keel which runs forward and down from the tip of the tooth, and then cuts back as a narrow ledge along the lingual margin. The overall shape of $P_3$ resembles a turned triangle with a long descending flat occlusal

surface flowing down distally. $P_4$ has a simpler triangular appearance with two cusp-like swellings distally. The molars resemble $P_4$ but the triangle is moved to the bucco-mesial side and a metaconid is added. In $P_4$ the cristid obliqua runs directly into the base of the triangular protoconid, whereas in the $M_1$, $M_2$, and $M_3$ it runs to the lingual base of the protoconid. A small centrally placed hypoconulid appears on $M_3$.

The teeth of *G. c. panganiensis* are similar *to G. c. lonnbergi*, except that $P^2$ and $P^3$ are just arrowhead paracones with minimal elaboration (no large stylids) whose overall shape is clearly distinct from *G. c. lonnbergi*.

For *Galago demidovii pusillus* $I^1$ and $I^2$ are short spindly pegs. $\underline{C}$ is somewhat tall and very straight, with a ledge of cingulum running from the mesial edge to a brief distal plateau. The $P^2$ is a smaller version of $\underline{C}$ and is slightly taller than $P^3$, which has a single arrowhead paracone with a massive lingual bulge for a tooth root. $P^4$ is completely molariform. The molars have massive hypocones, and the size grades down as follows: $M^1 – M^2 – P^4 - M^3$.

The toothcomb in *G. d. pursillus* has four slender central teeth and two larger lateral teeth. The $P_2$ at times resembles a very large lateral toothcomb slanted in an extremely procumbent fashion. $P_3$ tends to resemble $P_2$ but with a raised margin at the anterior end; on the distal end a plateau swings out to form a low descending lingual shelf which wraps back buccally on the anterior end to create the aforementioned raised margin. $P_4$ broadens the shape of $P_3$ and the edges of the distal plateaus are raised to resemble the hypoconids and entoconids of molars. $M_1$ completes

this pattern by adding a metaconid and squashing the protoconid to one side. The cristid obliqua runs into the base of the protoconid. There is a centrally placed hypoconulid on $M_3$.

The teeth of *Galago senegalensis* specimens tended to be very similar. $I^1$ and $I^2$ were small and skinny. C was a single stout cusp taller than the other teeth. $P^2$ and $P^3$ have triangular paracones with linguo-distal basins which is a common pattern for some lorisiform lower premolars. $P^4$ is molariform, and the hypocone on the molars almost resembles a disto-lingual stylid. The toothcomb has four slender central teeth and two larger lateral ones. Like *Galago demidovii* the $P_2$ sometimes resemble a very procumbent lateral toothcomb tooth or sometimes a less procumbent lateral toothcomb tooth with a strong mesial keel. $P_3$ is a triangular protoconid with a long distal slide into a posterior basin similar to the shape observed in *G. crassicaudatus lonnbergi*. The molars are typical for *Galago*. No striking regular differences help to sort out the subspecies of *Galago senegalensis.*

#### 3.1.1.1. Summary of Dentition for *Perodicticus*

The dentition of *Perodicticus* most closely resembles that of *Nycticebus*. The relative sizes of the teeth as well as the size and height and sharpness of the molar cusps of both *Perodicticus* and *Nycticebus* stand in sharp contrast to *Arctocebus*. In the former genera the molar cusps are low, rounded, and bulbous while in the latter taxon they are tall and sharp. *Arctocebus* and *Nycticebus* upper middle premolars are more likely to be double-cusped than *Perodicticus*. The canines of *Arctocebus* are much more straight (in profile as well as along the margins) than either

*Perodicticus* or *Nycticebus*. One specimen of *Nycticebus pygmaeus* (from Vietnam) at the USNM (# 256913) was observed to have a moderately developed finned bow on the lower caniniform anterior premolar, though the incidence of this condition among that genus is unknown. The only other similar feature observed was an extreme bowing of the mesial keels of the upper premolars in *Avahi laniger*. This taxon has extremely bowed fins on the upper canine and first two premolars, larger and more bowed far beyond anything observed in any of the lower anterior premolars of specimens of *Perodicticus*. In *Avahi* some degree of bowing can be seen on both the mesial *and* distal margins.

The members of *Perodicticus* can be distinguished dentally by: low, rounded cusps on their molars; having both I1 and I2 thicker and flatter than those of *Loris* or *Arctocebus* and more like the I1 of *Nycticebus*; a propensity for developing really small $M^3$s, sometimes as small as one-quarter or one-fifth the size of the other two upper molars.

### 3.1.2. Cranium

To appreciate the context of the detailed descriptions of the specimens of *Perodicticus* provided, a general overview of the features found in other similar taxa is provided, including specimens from *Loris*, *Nycticebus*, *Arctocebus*, and *Galago*.

In the *Loris* specimens well separated temporal lines run forward to the very massive rimmed orbits and meet medially in a very fine ridge. The rostrum is narrow and fairly tapered. The

zygomatic arch swings back, no wider than the orbits, and intercepts the confluence of the temporal ridge (raised temporal line) and nuchal line. The bone of the petrosal bulla is thin and transparent.

In the *Nycticebus coucang bengalensis* specimens the temporal lines often run together or very close to each other except for their arcs at both ends, whereas they tend to be further apart in *N. c. borneaus*. The snout doesn't taper as it does in *Loris*. It tends to be swollen on the sides from the roots of the upper canines, and a pair of prelacrimal fossae is often present to varying degrees of expression. The zygomatic arch in *N. c. begalensis* swings back a little wider than the orbits and stays mostly vertical/diagonal rather than forming a horizontal plateau as in *N. c. borneaus* or *Loris*. There is a much broader range of variation in the orientation of the zygomatic arch in the other *Nycticebus* taxa, yet in all observed cases the combined temporal-nuchal line running laterally is carried by the inflated petrosal bulla just a little lateral and inferior to the terminal plateau of the zygomatic arch. The bone of the petrosal bulla is thin, transparent, and mildly inflated.

In the *Arctocebus* specimens the temporal lines are generally well separated and there are no prelacrimal fossae on the longer, more slender snout. In *Arctocebus* the zygomatic arch does not contact the nuchal ridge because it ends in a horizontal plateau prior to the external auditory meatus. There is a dip over the meatus and then the skull swells out again posteriorly with an extremely swollen bulla.

In the *Perodicticus* specimens the snout tends to be shorter, stouter, and puffier as in *Nycticebus*. A prelacrimal fossa is often present but highly variable in expression. Also like *Nycticebus*, the temporo-nuchal ridge tends to end just below the terminal plateau of the zygomatic arch, except when excessive swelling of the bulla carries that ridge to an even more lateral and inferior position.

In the *Galago* specimens the skulls vary from a size comparable to *Nycticebus* and *Perodicticus* to a size closer to that of *Loris* or even *Arctocebus*. The temporal and nuchal lines meet, merge, and run onto a swollen bulla. However, the temporo-nuchal line and the bulla on which it rests are separated from the terminal plateau of the zygomatic arch by a gap over the external auditory meatus, as in *Arctocebus*. At times the posterior edge of the terminal plateau extends just over the meatus.

In *G. crassicaudatus lonnbergi* the snout is longer than *Nycticebus* and *Perodicticus* with a faint impression for prelacrimal fossae. The temporal and nuchal lines never rise to the level of ridge as they sometimes do in *Nycticebus* and *Perodicticus* despite similar overall size. In other *G. crassicaudatus* specimens a sagittal crest (line) may form at the meeting of the temporal lines. In *Galago demidovii* the temporal lines tend to be well-separated and the general proportions of the skull resemble *G. crassicaudatus*. In *Galago elegantulus elegantulus* there are moderate to deep prelacrimal fossae and the terminal zygomatic plateau doesn't extend at all over the external auditory meatus. *Galago senegalensis* is similar to *Galago elegantulus* and also developed moderate prelacrimal fossae. *Galago alleni* doesn't develop prelacrimal fossae.

#### 3.1.2.1. Summary of Cranium for *Perodicticus*

It is interesting to confirm that *Arctocebus* and *Galago* share a configuration of the lateral temporal region, that *Nycticebus* and *Perodicticus* share a pattern, and the pattern in *Loris* closely resembles that of *Nycticebus* and *Perodicticus*. However, *Perodicticus* cannot be distinguished based strictly on cranial morphology based on the results of this study.

### 3.1.3. Post Cranium

To appreciate the context of the detailed descriptions of the specimens of *Perodicticus* provided, a general overview of the features found in other similar taxa is provided, including specimens from *Loris*, *Nycticebus*, *Arctocebus*, and *Galago*.

In the *Loris* specimens there is no visible tail when viewing the pelage. The arms and legs are extremely long and skinny compared to the other lorisiform primates, and the highly slender body tapers considerably toward the caudal end.

In the *Nycticebus* specimens the bodies are large and long compared to *Loris* and especially *Arctocebus*. Some *Perodicticus* and *Galago* specimens approach the typical size of *Nycticebus*. There is typically no visible tail or just a tiny stub from the pelage view and unlike *Loris* the arms are thick and meaty. *N. c. bengalensis* tends be a little longer on average than *N. c. borneanus*. *N. c. hilleri*, and *N. c. javanicus* tend to be about the same size. *N. pygmaeus*, as the name implies, is much smaller than any of the specimens of *N. coucang*.

The *Arctocebus* specimens are smaller than all the specimens of *Loris* and *Nycticebus* with the exception of *N. pygmaeus*. The body proportions are similar to *Nycticebus* but on a smaller scale.

The *Perodicticus* specimens are approximately the same size as and have similar proportions to the *Nycticebus* specimens. Unlike *Loris*, *Nycticebus*, and *Arctocebus*, however, *Perodicticus* specimens have tails of appreciable length which are readily spotted in preserved skins as well as skeletal remains.

In the *Galago* specimens the tails are normally very long, sometimes twice as long as the span from the forelimbs to the hindlimbs. For specimens of *G. crassicaudatus* the bodies are similar in size to the larger specimens of *Perodicticus* (*P. p. ibeanus*), the size of a large domestic cat or small breed dog, with a very long and bushy tail twice the length of the body. *Galago demidovii* is about the size of an elongate hamster or a very skinny small rat with a tail as long as its body. *Galago senegalensis* is just a little larger than *Galago demidovii*, and *Galago alleni* is just a little larger than *Galago senegalensis*. The body of *Galago elegantulus elegantulus* looks like an amazingly skinny medium-sized potto with a very long bushy tail.

#### 3.1.3.1. Summary of Post Cranium for *Perodicticus*

It appears that the level of gross distinction of the general size and shape of the post-cranium tends to correlate most closely to the assigned taxonomic rank of species, which is unsurprising in and of itself as overall size and shape is commonly used in taxonomic assessments. It is

interesting though to note that *Perodicticus* and *Galago* share the distinction among extant lorisiforms of having tails of any appreciable length. *Perodicticus* has been distinguished post-cranially by having the longest tails of any of the lorisids, though the longest potto tail is far shorter than the smallest tail of a member of the taxon *Galago*.

### 3.1.4. Pelage

To appreciate the context of the detailed descriptions of the specimens of *Perodicticus* provided, a general overview of the features found in other similar taxa is provided, including specimens from *Loris*, *Nycticebus*, *Arctocebus*, and *Galago*.

In the *Loris* specimens the underside is very pale as is common for lorisiform primates. The face is similarly light colored except for dark rings around the eyes. The fur is darker on the dorsal side which goes lighter with red and yellow hues of brown toward the caudal end.

In the *Nycticebus* specimens the pelage varies to some degree. For *N. coucang bengalensis* the fur is light on the ventral side, on the arms and legs, and on the neck and face except for darker reddish patches around the eyes. This ruddy color runs back from the eyes as a pair of stripes that meet on the forehead and the resulting single stripe widens at the shoulders and runs medially before fading caudally. For *N. c. borneanus* the pelage is more uniform in color and tends toward tans and plain brown shades, with little or no light areas on the limbs or neck. Some more reddish-golden individuals do turn up. The pattern of darker redder fur around the

eyes running back into a dorsal stripe remains. For *N. c. coucang*, the pelage tends to be darker with dusty brown fur which may or may not have golden or reddish highlights and on which the dark dorsal stripe is abbreviated and poorly defined. *N. c. hilleri* has medium dark reddish fur with a reddish tent, a long dorsal stripe, and frosting about the neck and stripe. *N. c. javanicus* has somewhat lighter fur around the feet, hands, face and neck (vaguely similar to *N. c. bengalensis* but not as striking or consistent), with the basic pelage color light to medium reddish brown tones and a distinctly dark face and dorsal stripe. *N. pygmaeus* has a reddish pelage with a darker red dorsal stripe and light frosting occasionally sprinkled around the stripe.

The *Arctocebus* specimens have light brown fur with heavy golden and reddish tones. The pelage is fairly uniform yet slightly lighter around the face.

In the *Perodicticus* specimens there is a great deal of variation in the pelage except for the dark midline dorsal stripe. The different colors and patterns for pottos will be described in detail in the following sections.

In *Galago* specimens vary considerably. For specimens of *G. crassicaudatus lonnbergi* the pelage is a thick brown fur tipped with reddish gold highlights except around the head and neck, which have shorter hairs. The tail fur is all golden brown with a slight reddish tint. In *G. crassicaudatus panganiensis* there are muted tan tones on the top of the hairs with dark or black toward the skin. The fur is short rather than long and bushy in *G. c. lonnbergi*. Kenya specimens are closer to a plain brown color, but sometimes they are uniformly ruddy. Examining other specimens attributed to *Galago crassicaudatus*, such as *G. c. crassicaudatus*,

*G. c. garnetti*, *G. c. lasiotis*, and *G. c. kikuyensis*, the patterns seen in *G. c. lonnbergi* and *G. c. panganiensis* are present but not always exclusively distributed by taxa.

For specimens of *G. demidovii pusillus*, the uniform coat varies from reddish tan to dusty brown to dark brown, with a small thin vertical light stripe between the eyes. In *Galago elegantulus elegantulus* the ventral pelage is dark grey mixed with lighter fur in a salt and pepper mix which tends to creep up onto the sides especially on the limbs. The dorsal side is dusty brown covered by reddish golden tints which become especially strong on the central part of the torso. There is a very brief deep red dorsal stripe. In *Galago alleni* the pelage is dark brown with mild dark gold and red tipping.

In the species *Galago senegalensis* many interesting patterns emerge. *G. s. albipes* and *G. s. braccatus* are dusty grey brown with a tendency for yellow around the limbs, especially around the legs. The tails are reddish. Similarly, *G. s. granti* and *G. s. moholi* are somewhat similar, possessing a mottled pelage. The mix is dark and gold for *G. s. granti* (darker reddish colors toward end of tail) and dusty grey and light tan for *G. s. moholi* (with a rosy shade of brown for the tail). Some specimens of *G. s. moholi* do get some yellowing around their legs giving a slight resemblance to *G. s. albipes* and *G. s. braccatus*.

All the subspecies have reddish colored tails (though the general light grey color of *G. s. moholi* makes it rosier in appearance). *G. s. albipes*, *G. s. moholi*, *G. s. senegalensis*, and *G. s. sotikae* tend to have dusty grey or plain brown pelages. *G. s. braccatus* is similar but has extensive golden-yellow about the arms and legs. *G. s. albipes* and *G. s. sotikae* also show some of this

yellow to varying degrees, more so on the hindlimbs. *G. s. moholi* and *G. s. senegalensis* tend to have a lighter off-white coloration limbs though some yellowish specimens were observed. *G. s. moholi* has a dusty grey and light tan mottled pelage. *G. s. granti* and *G. s. zanzibaricus* have reddish overcoats occasionally mottled with dark brown.

For the sake of comparison of the degree of difference between pottos and others closely related primates as well as the degree of difference recognized as taxonomically relevant in other genera some non-*Perodicticus* specimens are shown below. A skin from the other African lorisid genus, *Arctocebus*, is included (Figure 1). In addition to major differences in size and dental morphology there is a very distinct difference in pelage compared to *Perodicticus*. These differences can be compared to different members of the species of one of the Asian lorisids genera, *Nycticebus* (Figure 2). The size and pelage differences present in these different species of *Nycticebus* are comparable to the same differences in the subspecies of *Perodicticus potto*. On the other hand, the subspecies of *Galago demidovi* shown (Figures 3 and 4) have been elevated in some taxonomies to the level of (cryptic) species, despite their outward similarity in appearance.


**Figure 1 Pelage of a specimen from the genus *Arctocebus***

**Figure 2 Pelages of some of the different taxa within the genus *Nycticebus*. From top to bottom: *N. coucang javanicus, N. coucang coucang, N. pygmaeus*. *N. c. javanicus* was once labeled as a species, *N. javanicus*.**

**Figure 3 Pelages of the subspecies of *Galago demidovi*. The top is *G. d. demidovi* and the bottom is *G. d. anomurus***

**Figure 4 Another comparison of the pelages of subspecies of *G. demidovi*. The top is *G. d. murinus* and the bottom is *G. d. anomurus***

### 3.1.4.1. Summary of Pelage for *Perodicticus*

It appears that the level of gross distinction of the general color and pattern of the pelage tends to correlate most closely to the assigned taxonomic rank of subspecies, which is unsurprising in and of itself as major markings and patterns are commonly used in taxonomic assessments. There is no major distinguishing feature of the pelage for *Perodicticus*.

## 3.2. Taxa Within *Perodicticus*

The descriptions and measurements previously given for taxa within the genus *Perodicticus* are summarized here. These descriptions are the basis for the taxa recognized within the genus and by extension the basis for testing the validity of those same taxa. The information for each taxon is broken down into dentition, cranium, post cranium, and pelage. Potentially taxon defining features are then summarized. These form the basis of testing traditional taxa by comparing predicted versus observed features described for the specimens attributed to the both the genus *Perodicticus* and then to a sub-taxon of *Perodicticus*.

### 3.2.1. *P. p. edwardsi*

#### 3.2.1.1. Dentition

The only information on dental features of the taxon designated as *P. p. edwardsi* comes from dental measurements made by Ernst Schwarz. The dental measurements (in mm) provided by Schwarz (1931a), based on 12 specimens, include the length of the tooth row from C-$M^3$ and listed a maximum value at 24.3, a minimum value at 21.7, and an average value of 22.9. The measurements also included the length of the tooth row from $M^1$ to $M^3$ with a maximum value of 11.4, a minimum of 8.6, and an average value of 10.0. The measurements suggest the cheek teeth are, like *P. p. faustus* (whose average $M^1$-$M^3$ length was placed at 10.2 mm), much larger than any other subspecies of *Perodicticus* (whose averages for $M^1$ to $M^3$ length were around 8.8 mm). It should be noted that these measurements were based on examining six specimens

attributed to *P. p. potto*, forty four specimens attributed to *P. p. edwardsi*, two specimens attributed to *P. p. faustus*, and thirty four specimens attributed to *P. p. ibeanus*.

The only potentially distinguishing dental feature for *P. p. edwardsi* is the presence of molar teeth which are very large compared to the other specimens of *Perodicticus*. It shares this described feature in the traditional taxonomies, however, with *P. p. faustus*.

#### 3.2.1.2. Cranium

The cranial measurements (in mm) provided by Schwarz (1931a), based on 12 specimens, include the greatest length (maximum 68.0, minimum 63.1, average 65.8). He identified no type specimen for his measurements. According to Schwarz's published data, *P. p. edwardsi* has the largest average maximum cranial length with *P. p. ibeanus* having the second largest average maximum length at 63.9 mm, whereas *P. p. potto* at 61.4 mm and *P. p. faustus* at 61.6 mm had the smallest values.

Hill (1953) describes the squamosal region of the zygoma as well as the adjacent mastoid region as being very broad, but that does not provide a reasonable basis for distinguishing taxa.

#### 3.2.1.3. Post Cranium

There is little or no specific information published on the post-cranium of this taxon.

#### 3.2.1.4. Pelage

The only reference to pelage by Schwarz (1931a) for this taxon is to a juvenile with a silvery coat whose head is more brown in color.

Hill (1953) comments that the taxon is described as "rich red, almost mahogany. Hands and feet dark brown, either uniform with or darker than the general colour of the upper parts. Bristle hairs about nape strongly developed…Juveniles with silvery coat" (193).

#### 3.2.1.5. Distinguishing Features of the Taxon

Whereas having very large cheek teeth relative to other specimens of *Perodicticus* is descriptive of *P. p. edwardsi*, it is also descriptive of *P. p. faustus*. In fact, *P. p. faustus* is considered a synonym for *P. p. edwardsi* in contemporary literature. However, *P. p. edwardsi* is also described as having the largest values for maximum cranial length, whereas *P. p. faustus* is listed as ranking with *P. p. potto* in having the smallest average values for this measurement.

### 3.2.2. *P. p. faustus*

#### 3.2.2.1. Dentition

The dental measurements (in mm) provided by Schwarz (1931a), based on 2 specimens, include the length of the tooth row from C-$M^3$ (maximum 22.3, minimum 22.3, average 22.3) and from $M^1$-$M^3$ (maximum 10.2, minimum 10.2, average 10.2). The sample for these values includes

measurements taken from the type specimen of *P. p. faustus* (B.M. 11.10.19.9). Hill (1953) suggests that the molars are larger than those of *P. p. potto*.

As previously noted, *P. p. faustus* shares the description of having large cheek teeth (relative to other pottos) with *P. p. edwardsi*. The study of dental eruption by Schwartz (1974) points to a major developmental difference between those specimens labeled *P. p. faustus* and *P. p. edwardsi* and those specimens labeled *P. p. ibeanus*. *P. p. ibeanus* differs from the former group in "1) a generally earlier appearance of the permanent dentition, 2) the appearance of the upper incisors prior to, rather than at the same time as, the toothcomb, 3) the appearance of $P_4$ and then $P_3$ prior to, rather than after, $P^4$ and then $P^3$, respectively, 4) the appearance of the upper canine prior to, rather than after, $P^2$, and 5) the appearance of $M^3$ prior to, rather than after, $P^4$" (Schwartz 1974:98).

#### 3.2.2.2. Cranium

The cranial measurements (in mm) provided by Schwarz (1931a), based on 2 specimens, include the greatest length with a maximum value of 61.6, a minimum value of 61.6, and an average 61.6, which was the value taken from the type specimen (B.M. 11.10.19.9). This is far below the 65.8 mm average listed *for P. p. edwardsi*.

The skull is described by Hill (1953) as being larger than *potto* but smaller than *edwardsi*.

#### 3.2.2.3. Post Cranium

There is little or no specific information published on the post-cranium of this taxon.

#### 3.2.2.4. Pelage

The description provided by Schwarz (1931a) based on a juvenile and is recorded as "bright cinnamon-brown, the long hairs being black, and the general effect therefore quite distinct from the type" (253). The type description is not included but it is the only other specimen examined by Schwarz for this taxon.

Hill (1953) reports, "Colour variable as in other races, generally bright cinnamon-brown with long black hairs interspersed" (193).

#### 3.2.2.5. Distinguishing Features of the Taxon

As mentioned under the description of *P. p. edwardsi*, both *P. p. edwardsi* and *P. p. faustus* share the description of having the largest cheek teeth among pottos, but *P. p. edwardsi* is listed as having the largest values from maximum cranial length and *P. p. faustus* is listed as having among the smallest values for that measurement. Both taxa also share the description of having very reddish fur.

### 3.2.3. *P. p. ibeanus*

#### 3.2.3.1. Dentition

The description of *Perodicticus ibeanus* (syn. *P. potto ibeanus*) includes the following account of the teeth: "Canines rather slender. Anterior premolar long, pointed, two-thirds the height of the canine. Other cheek teeth all very small; second molar smaller than the first. Anterior lower premolar longer than posterior" (Thomas 1910b:536). This original description of the dentition of *P. p. ibeanus* includes (in millimeters) the "length of cheek-tooth series 16.5; of molars only 8.5; breadth of $m^1$ 3.8, of $m^2$ 3.2" (Thomas 1910b :536).

The dental measurements (in mm) provided by Schwarz (1931a), based on 34 specimens, include the length of the tooth row from C-$M^3$ and gives a maximum value of 23.0, a minimum value of 18.3, and an average value of 20.9. The length from $M^1$-$M^3$ yielded a maximum value of 9.8, a minimum value of 7.6, and an average value of 8.8. The type specimen of *P. p. ibeanus* (B.M. 10.3.18.1) is recorded by Schwarz (1931a) as having a tooth row length of 20.0 mm from C-$M^3$ and 8.3 mm from $M^1$-$M^3$. The average values of these measurements place *P. p. ibeanus* in a small size group with *P. p. potto* as opposed to the large size group of *P. p. edwardsi* and *P. p. faustus*.

Hill (1953) also describes *P. p. ibeanus* as having small teeth.

#### 3.2.3.2. Cranium

The dimensions of the skull recorded for the type specimen of *P. p. ibeanus* are "upper length 64 mm.; basal length 55; greatest breadth 46; nasals 14.2 x 5.3; interorbital space 9.3" (Thomas 1910b:536).

The values recorded for the type specimen by Schwarz (1931a) include the greatest length (63.7 mm).

The cranium of the type specimen for *P. p. ibeanus* was described as "large as in P. batsei (sic), but the teeth small as in P. potto (sic). Nasals very short" (Thomas 1910b:536).

#### 3.2.3.3. Post Cranium

The post-cranial description of the type specimen of *P. p. ibeanus* includes the following measurements, "Head and body 339 mm; tail 68; hind-foot 76" (Thomas 1910b:536).

The post-cranial description of the type specimen of *P. p. ibeanus* includes a longer tail than other pottos (Thomas 1910b:536).

#### 3.2.3.4. Pelage

The pelage description of the type specimen of *P. p. ibeanus* includes "long-haired," "blackish anteriorly, grey posteriorly," "fur soft and thick" (Thomas 1910b:536). More specifically:

"General colour grizzled ashy, but the shoulders and fore-back blackish; the contrast between the two colours very marked. Head brownish clay-colour, the extreme tips of the hairs blackish; these black tips broadening posteriorly so as to make the nape and forequarters almost black, with a hidden suffusion of dark clay-colour. The long bristle hairs of the crown and nape black. Rest of the body, behind the withers, grizzled ashy, the longer hairs dark with grayish-white tips, the woolly undefur dark slaty basally, the broadly clay-coloured, and with dark tips. Under-surface grayish white, not sharply defined, the hairs slaty basally, dull grayish white terminally (grey no. 8). Arms and legs grizzled ashy like the body; hands and feet buffy brownish. Tail comparatively long, cylindrical, ashy grey" (Thomas 1910b:536).

The pelage is in fact listed by Thomas as the distinguishing feature of this type of potto: "*P. ibeanus* is at once distinguishable from all others by the hoary colour of its back, which contrasted markedly with its blackish shoulders, the difference being due to the long hairs of the former being tipped with ashy, a character not found in any other Potto" (Thomas 1910b:537).

The description offered by Schwarz (1931a) for the type specimen of this taxon is "hoary black", while others are described as "pale yellowish brown." (254).

Hill (1953) describes a "dense, soft, woolly coat in which both wool hairs and bristle hairs are proportionately longer than in the lowland forms" (193). He elaborates:

"Dark, almost blackish, colour of forepart of back contrasted with grayer posterior parts. Head brownish, with the hairs black-tipped; remainder grizzled ashy-grey; hairs with slaty bases. Under parts grey with slaty bases to hairs. Hands and feet buffy-brown; tail ashy…Juvenile woolly-coated, whitish, washed with faint cinnamon above, under parts, including neck, grey" (193-195).

#### 3.2.3.5. Distinguishing Features of the Taxon

Dentally, *P. p. ibeanus* has been described as being distinct in having the second upper molar smaller than the first. Post-cranially it is supposed to have a relatively long tail. However, the primary distinguishing feature listed for this taxon is the pelage, which has a head of one color, a field of darkened to black fur across the shoulders, and then a third color for the rest of the trunk and tail.

### 3.2.4. *P. p. ju-ju*

#### 3.2.4.1. Dentition

The description of the type specimen of *P. p. ju-ju* includes (in mm) "upper cheek-tooth series 17.8; molars 9; breadth of $m^2$ 4.1" (Thomas 1910a:352).

The type specimen of *P. p. ju-ju* (B.M. 2.7.12.1) is recorded by Schwarz (1931a) as having a tooth row length of 21.4 mm from C-$M^3$ and 8.7 mm from $M^1$-$M^3$.

The teeth of the original type specimen are described as being small relative to other pottos, similar to *P. p. ibeanus* but differing in having $M^2$ equal in size to $M^1$ (Thomas 1910a). In addition, "$P^2$ similarly [to *P. p. ibeanus*] two-thirds the height of the canine and longer than the teeth following it, and below the same," (Thomas 1910a:352).

Hill (1953) makes a brief comment about the dentition of *P. p. ju-ju*, stating that they are similar in *P. p. potto* in having small teeth, "especially the anterior premolars" (192).

#### 3.2.4.2. Cranium

The dimensions of the skull reported for the type specimen of P. p. ju-ju are (in mm) "upper length 66; basal length 58; greatest breadth 47; nasals 17" (Thomas 1910a:352).

The values recorded for the type specimen by Schwarz (1931a), the only specimen examined, include the greatest length (66.6 mm).

The description of the cranium of the type specimen is brief, "Skull rather larger than that of *P. potto*; nasals of about the same length, longer than in *P. ibeanus*. Postorbital bar about as in *P. batesi*; broader than in *potto*, narrower than in *ibeanus*" (Thomas 1910a:352).

### 3.2.4.3. Post Cranium

The post-cranial description of the type specimen of *P. p. ju-ju* includes the following measurements, "Head and body 355 mm; tail 75; hind foot 77" (Thomas 1910a:352).

The post-cranial description of the type specimen of *P. p. ju-ju* suggests it has a proportionally long tail (Thomas 1910a:352).

### 3.2.4.4. Pelage

The pelage of the type specimen of *P. p. ju-ju* is described thus:

"Fur close and woolly, much shorter than in *P. ibeanus*. Bristle-hairs practically absent. General colour above 'drab-grey,', the other three W. African Pottos being of a more rufous brown colour. Whole of back uniform, without any darker colour on the foreback. Underfur grey at base (grey no.6), then dull buffy whitish, the ends dark brown; the few longer hairs with light tips, not affecting the general colour. Under surface well-defined greyish white, the hairs grey basally, white terminally. Outer surface of arms and legs drab-grey like back, inner surface whitish like belly, but becoming more drabby towards wrists and ankles; hands and feet drab grey above" (Thomas 1910a:352).

Thomas considers the pelage important in distinguishing *P. p. ju-ju* from *P. p. potto* and *P. p. ibeanus*.

Hill (1953) notes that additional materials indicate the hands and feet may be paler than the back, but otherwise agrees with the description of the pelage offered by Thomas.

#### 3.2.4.5. Distinguishing Features of the Taxon

While the teeth of *P. p. ju-ju* are described as being similar to the teeth of *P. p. potto*, the skull of *P. p. ju-ju* is supposed to be considerably larger than that of *P. p. potto*. In addition, *P. p. ju-ju* is described as having a proportionally long tail. This is interpreted here as meaning relatively long for a potto of a particular body size. The pelage is also supposed to be distinctive, a drab grey with no appreciable dark patch on the upper back.

### 3.2.5. *P. p. potto*

#### 3.2.5.1. Dentition

In the description of the type specimen of *P. ju-ju* (syn. *P. p. ju-ju*), a comparison to *P. potto* (syn. *P. p. potto*) is made with regard to the dentition—"In *P. potto* $p^2$ is but a little larger than $p^3$ above, and is smaller than it below. The molars are also even smaller [than *P. ju-ju*]" (Thomas 1910a:352).

The dental measurements (in mm) provided by Schwarz (1931a), based on 6 specimens, include the length of the tooth row from C-$M^3$ with a maximum value of 21.3, a minimum value of 18.1, and an average value of 20.0. Measurements from $M^1$-$M^3$ yielded a maximum value of 8.7, a

minimum value of 7.9, and an average value of 8.3. These were the smallest average values Schwarz recorded for specimens of *Perodicticus*.

The description presented by Hill (1953) includes the following comment, "Chiefly distinguished from other races, notably the fact that the foremost lower premolar is noticeably smaller than its successors; this applies to some extent to the corresponding upper tooth" (192).

#### 3.2.5.2. Cranium

The cranial measurements (in mm) provided by Schwarz (1931a), based on 6 specimens, include the greatest length (maximum 63.6, minimum 60.5, average 61.4). The greatest cranial length for the chosen topotype specimen (B.M. 13.10.4.1) was 60.5 mm.

Hill (1953) describes the nasal bones as being very long (longer than *P. p. ibeanus*) with a post-orbital bar width larger than *P. p. potto* but smaller than *P. p. ibeanus*.

#### 3.2.5.3. Post Cranium

The description of the taxon by Hill (1953) includes the remark that the tail is relatively longer in *P. p. potto* than in the eastern races.

### 3.2.5.4. Pelage

One distinction Thomas (1910a) makes between *P. p. potto* and *P. p. ju-ju* is the dark brown color of the fur of the former. Schwarz (1931a) feels he is unable to "define external racial characters" for this taxon (251).

Hill (1953) gives the following description:

> "Colour of upper parts rich reddish-brown with a dark (almost black) spinal stripe fading posteriorly but wide on interscapular region; hands and feet pale, in contrast with upper parts. Bases of hairs silver-grey…Juveniles darker, reddish-brown above, more rufous on back of the head and neck, darker on shoulders; beneath creamy white washed with rufous; bases of hairs silver-grey, tips reddish-brown" (192).

### 3.2.5.5. Distinguishing Features of the Taxon

Dentally, the descriptions distinguish *P. p. potto* by suggesting that $P^2$ is a little larger than $P^3$ while $P_2$ is a little smaller than $P_3$. In similar description, the "foremost" of the lower premolars is supposed to be smaller than those teeth that follow it. Given that the caniniform tooth situated disto-laterally from the toothcomb is considered to be a premolar, designated $P_2$, in this study it is presumed that the $P_2$ or foremost premolar is what is described in the data sections as $P_3$ or the middle lower premolar. Also, *P. p. potto* is supposed to have the smallest molar teeth, even smaller than *P. p. ju-ju*.

# 4. DENTITION

## 4.1. Non-Metric Data

The general description of the dentition of the genus *Perodicticus* was described by Schwartz and Tattersall (1986), and was reviewed in more detail by Schwartz and Beutel (1995). Current general observations are provided here.

The upper dentition is typical of the lorisiform primates, with two spindly peg-like teeth in the incisor position per side. In some cases there is a gap between these teeth in the same side, but they are just as likely to be pressed together with no gap. There does not appear to be any localized or regional pattern to these differences.

The upper canine is always very large relative to the rest of the teeth, though the size does tend to vary, especially in the length of the tooth. It is somewhat bladelike and in pristine condition tends to have slight mesial and distal crests which barely rise above the plane of the slender crown.

The anterior upper premolar is always the largest premolar and often resembles the canine. In some cases it is as slender and nearly as long as the canine, with a severe drop in height from this tooth to the middle premolar. In other cases, the peak of the crown is not far above the

shoulders, giving a stepwise appearance from the canine to the first premolar to the second premolar. This difference was one of the major features noted in the review by Schwartz and Beutel (1995).

The middle and posterior upper premolars are roughly the same height and are banded by a mild cingulum. In some specimens the middle premolar is noticeably smaller than the rest of the tooth row, including the posterior premolar. This feature has a particularly high frequency of occurrence in a small part of the western region of pottos' range. In addition the middle premolar sometimes "wings" or appears to be rotated out of its mesio-distal axis alignment, sometimes 45 degrees out of place (mesial edge rotated buccally). The shape of the premolars resembles an arrowhead or fat spear point, an oblong diamond that is somewhat elongated toward the tip. The middle premolar is often gently swollen on the lingual side and only in one case was it observed to rise and become distinct enough to resemble a protocone cusp. On the posterior premolar the development of a minor lingual protocone (somewhat heel-like in appearance) is the common condition.

The first and second upper molars appear to be an elaboration on the premolars. In pristine form the paracone and metacone resemble two arrowheads put together with the protocone and hypocone arising in the same form as it appears on the posterior premolar but larger. Despite the arrowhead appearance of the paracone and metacone in unworn teeth they are still low and rounded. The notch separating the hypocone from the trigon and the heel-like extension beyond it are both weakly developed, as are the pre- and postprotocristae. The first molar may be larger, the same size, or smaller than the second molar.

The third upper molar is highly variable. It can be one-fifth the size the other molars or nearly two-thirds their size. In some cases it is still a miniature version of the larger molars, with three identifiable cusps of the paracone-protocone-metacone trigon, while in other cases it has only a paracone and protocone, severely compressed along the mesio-distal axis and appearing like a squashed posterior premolar.

The lower dentition has two central teeth and a thicker lateral tooth on each side of its procumbent tooth comb. The tooth distal to the toothcomb, commonly labeled the lower anterior premolar, is caniniform in shape. In most specimens it resembles a somewhat shorter and bulkier version of the true upper canine with a minor crest along its mesial and distal margins. However there is also a tendency in some specimens for the mesial crest to swell out to varying degrees. In many cases this bowed crest begins to resemble a fin before swinging lingually and distally along the lower base of the crown and forming the lingual border of a small distal extension of the tooth (see figure 10). This fin can either be mild or strong. A bowed fin is never observed on the distal margin. This feature is almost completely localized to the western region of the pottos' range.

The middle and posterior lower premolars are unlike their upper jaw counterparts. It is as if they have the basic arrowhead shape with a good deal of elaboration. This elaboration comes in the form of a lingual to linguo-distal or even distal bulky extension extending out from the arrowhead. The keels on the mesial and distal margins of the arrowhead tend to continue on as raised ridges and wrap down and around the tooth the form the mesial and distal lingual borders

of the extension, which frequently resembles a sloping or broken plateau. Another ridge may or may not arise from the tip of the arrowhead and diverge from the ridge of the distal keep as it runs in a loosely disto-lingual direction. This middle ridge and the distal ridge curving back in a mesio-lingual direction form lingual and buccal sides (respectively) of the distal border of the extension. As these ridges run down the distal side of the protoconid they may trace out a distally-oriented concavity which is sometimes tear-shaped. This tear-shaped depression on the lower premolars was a feature named and highlighted in the review by Schwartz and Beutel (1995). It should be noted that there is a great deal of variation in this trait, with the angle at which the arrowhead is facing and the subsequent size and orientation of the extension being unpredictable from specimen to specimen. The arrowhead can be aligned along the mesio-distal axis or turned with the "mesial" edge (for reference) rotated out toward the buccal margin up to 45 degrees (typically) or in some cases closer to 60 or 70 degrees. In some cases the extension is extremely small, poorly defined and bounded; with heavy wear to the arrowhead portion the extension may be practically indistinguishable or identifiable. The lower middle and anterior premolars tend to be the same size, but in some cases the middle premolar is noticeably shorter and the distal extension is always longer/more noticeable on the posterior premolar. While this extension may be practically absent from the middle premolar it is always readily observed (in various conditions of preservation) on the lower posterior premolar. The reduced size of the lower middle premolar occurs frequently with the reduced upper middle premolar and like that trait it is highly concentrated in a small area of the western range of the pottos.

The lower first and second molars are often similar in size, with one or the other a little larger or smaller. Five very low, rounded, and bulbous cusps (protoconid-metaconid trigonid and

hypoconid-entoconid-hypoconulid talonid) are readily identified. The protoconid and hypoconid are fatter while the metaconid and entoconid are somewhat thinner and in many specimens they are compressed along the bucco-lingual axis. These compressed cusps are often pressed into a wall of enamel formed by a crest running along the lingual margin of the occlusal surface. The entoconid tends to be diminished in size, and brief cristid obliqua drifts from a more central course toward the meeting of the metaconid and protoconid to a course toward the metaconid.

The lower third molar is not as variable in shape as its upper jaw counterpart but it shares the range of size difference. The notable exception is that in a few specimens the third molar was as large as the other two molars, which was never observed in the upper third molar. The shape of the third molar is determined by its size. Smaller third molars appear to be budding into the same shape as the first two lower molars but have been locked into an earlier state of expression. In one specimen an extra molar behind the lower third molar was observed. As is the case for third molars of extremely small size, it was poorly developed.

The description of two main morphotypes in the upper canine to premolar series by Schwartz and Beutel (1995) was not assigned to any particular taxonomic scheme, but their presence has been confirmed (Figures 5 and 6). The one pattern has a step-wise reduction in size from the upper canine through the premolars, whereas the other has a major difference in size between the canine and the first premolar and then between the first premolar and the rest of the cheek tooth series.

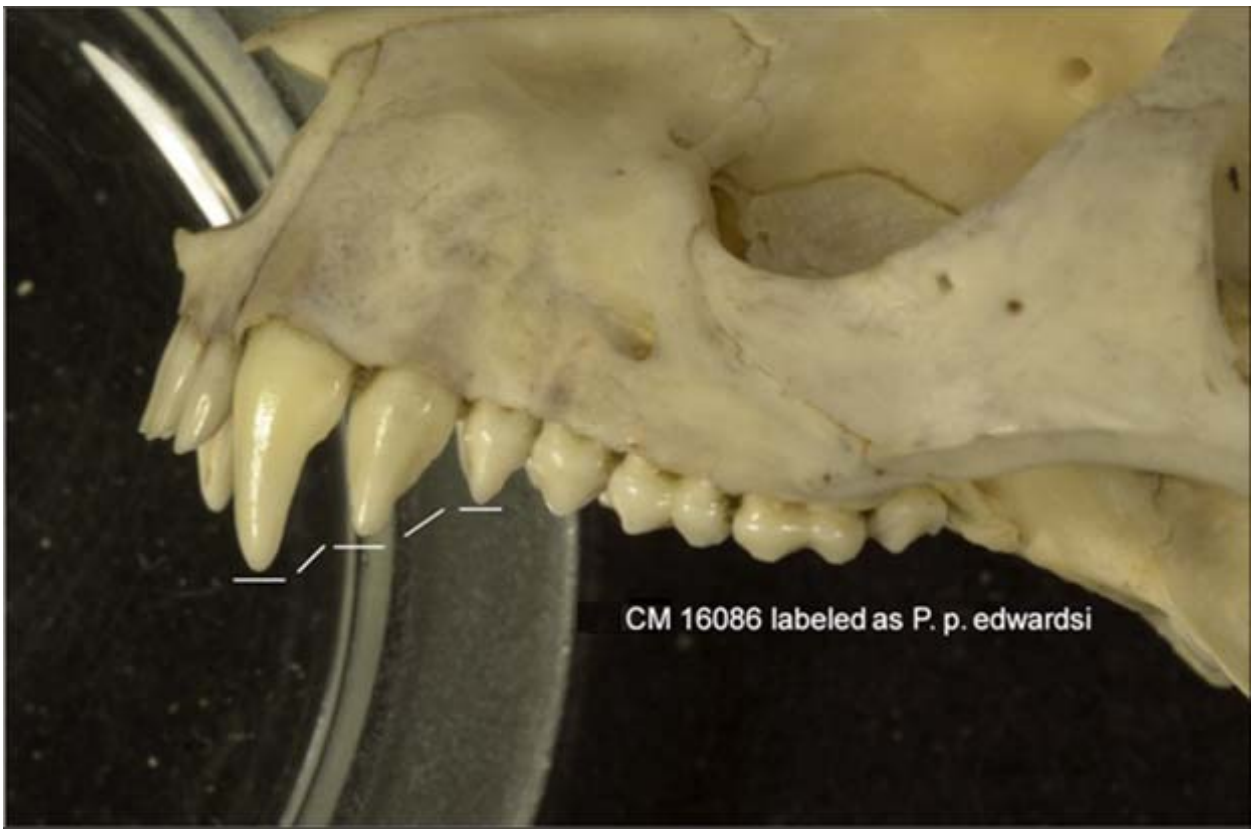


**Figure 5 Stepwise appearance of canine-premolar series**

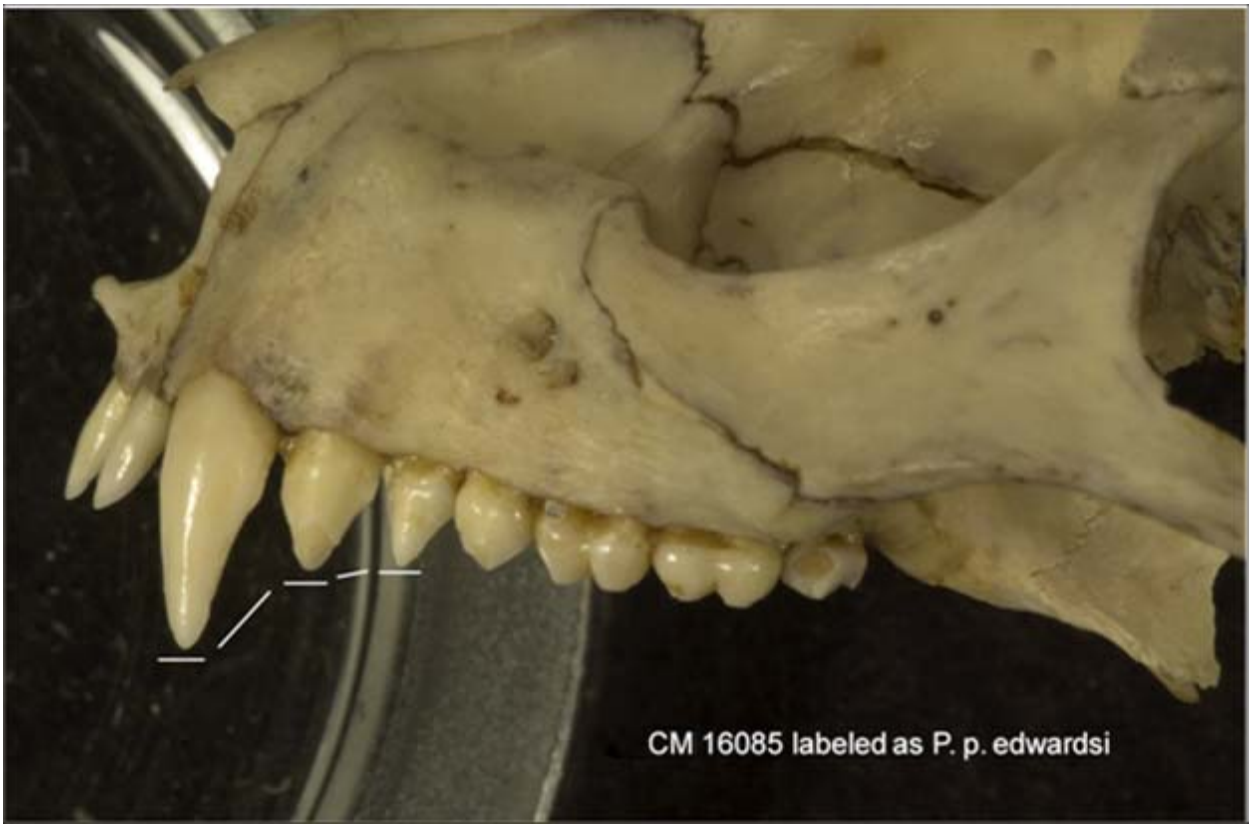


**Figure 6 No stepwise pattern of canine-premolar series**

However, these patterns seem to be distributed broadly rather than being geographically localized or concentrated. Further analysis may show further correlation of these morphological states to other genetic, morphological, or ecological conditions.

The western pottos, as Hill (1953) indicated, do display a tendency to have a highly reduced premolar (Figure 7). Yet there is a question as to the identity of this tooth. In the lower tooth row the large caniniform tooth is generally considered to be the first premolar, which would make the tiny tooth the middle, and not the first, premolar. In the upper tooth row, the large caniniform tooth is considered to be a canine, and the corresponding tiny upper tooth is also considered the middle premolar. It should be noted, however, that the tendency to have one or

both of these teeth (upper and lower middle premolars) highly reduced appears to be centered geographically around (but not exclusive to) specimens from Ghana and the Ivory Coast.

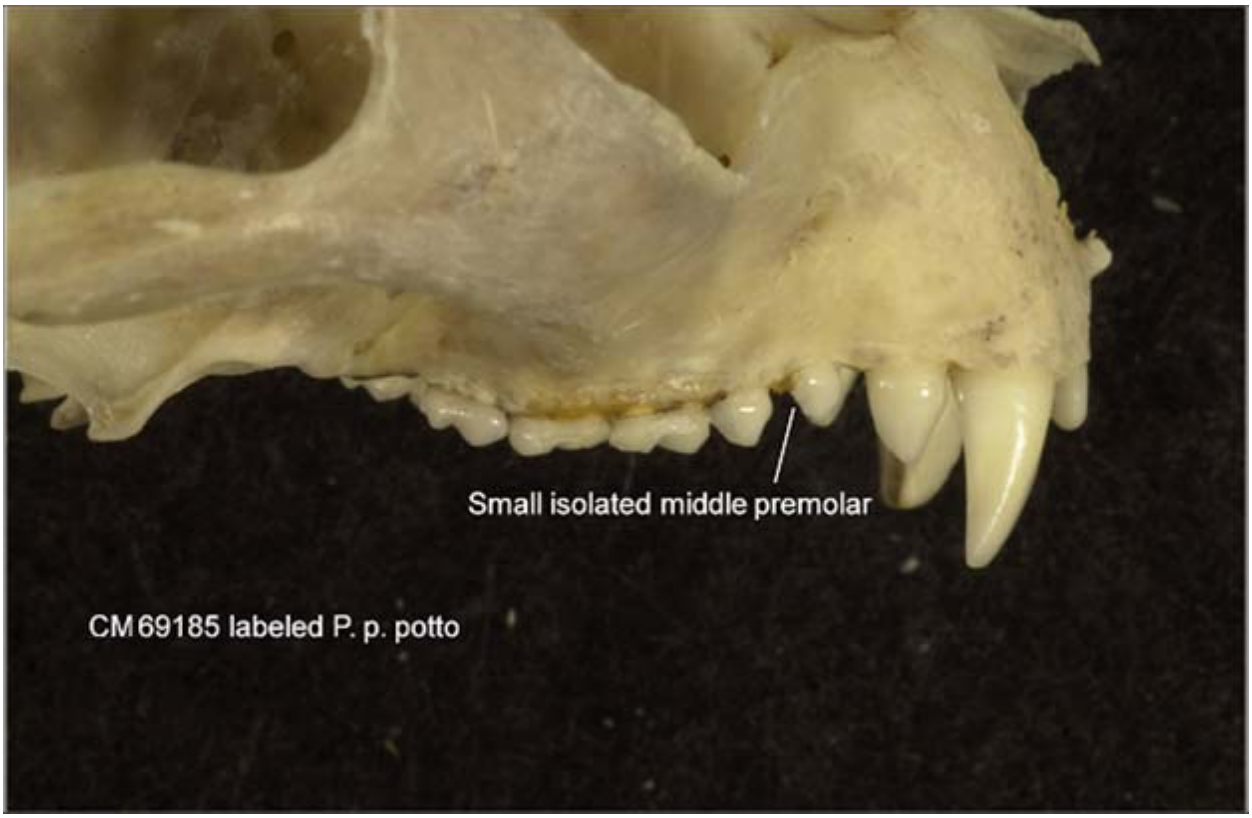


**Figure 7 Small isolated middle premolar**

In addition, there is a heretofore undescribed feature which distinguished specimens from the western range of *Perodicticus*, including those with the tiny middle premolars. This feature is an excellent indicator that the specimen in question comes from the western range. On the lower (caniniform) anterior premolar, on the mesial side, the normal keel which is present on both the mesial and distal sides becomes greatly expanded and flares out into a bow-shaped fin (compare Figures 8 and 9 to Figure 10).

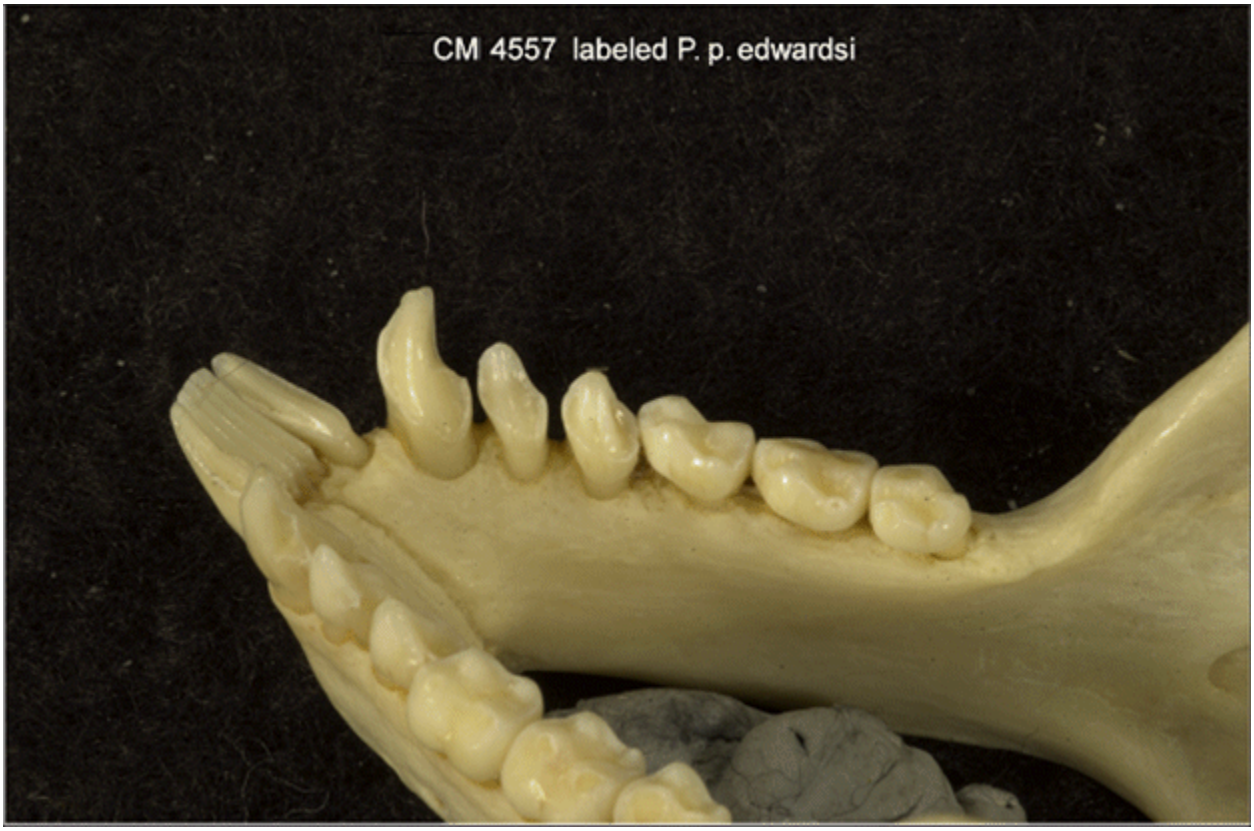


**Figure 8 No bowed fin on lower anterior premolar**


**Figure 9 No bowed fin (different specimen and angle)**

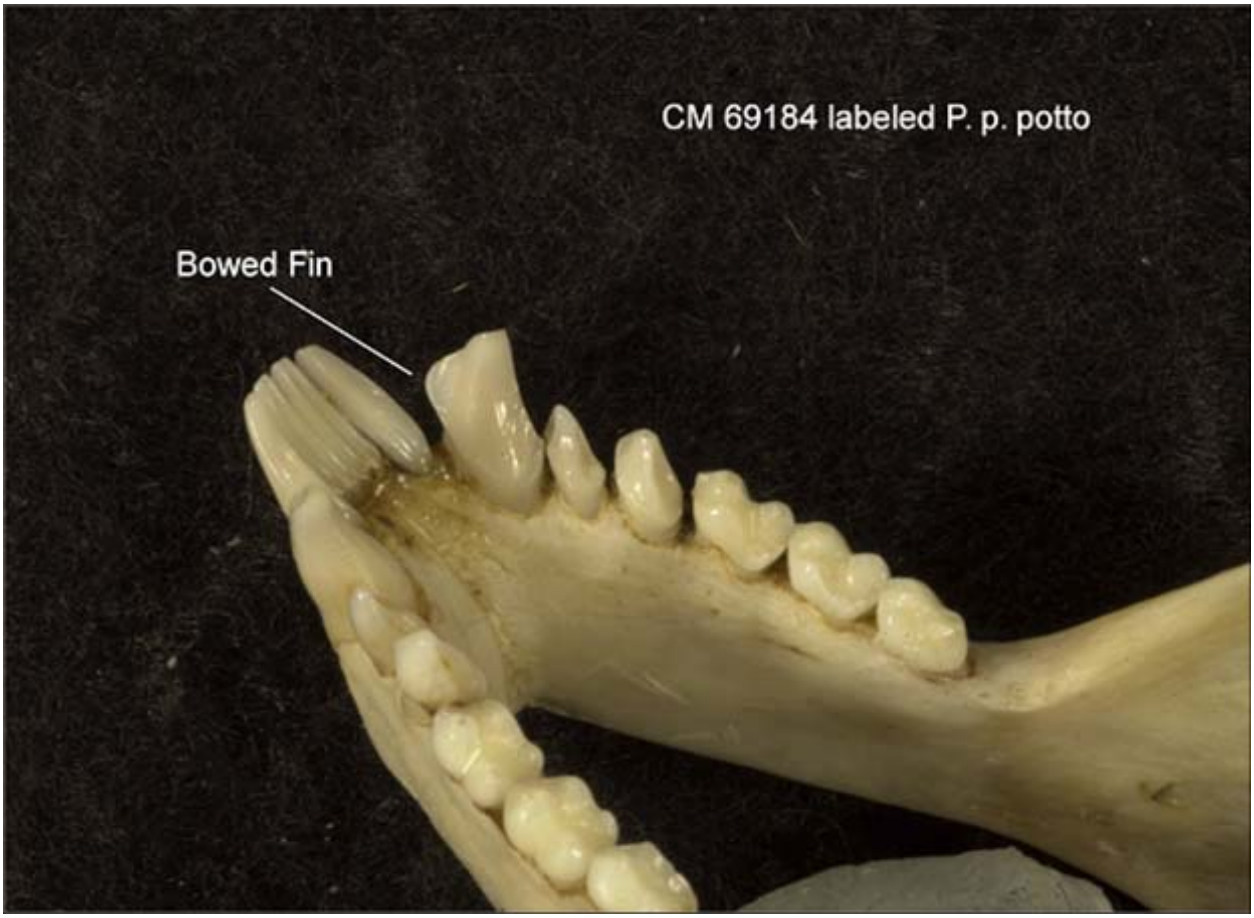


**Figure 10 Bowed fin present on lower anterior premolar**

The bowed fin trait exhibits variability, so that some weaker specimens may be hard to positively identify, but they tend to be fairly strong and reliable. The teeth are typically worn at an oblique angle in which the slope rises distally. This likely indicates that this fin has been rubbing consistently against a hard surface at the same angle, and it is not unknown for lorisids to gnaw on trees to extract exudates. However, pottos are usually listed as being opportunistic with regard to the availability of gums and saps rather than chewing through bark (Alison 1985).

## 4.2. Metric Data

### 4.2.1. View of the Data by Sex

There was sexual dimorphism in the pooled sample, particularly in the length of the upper and lower second molars.

Table 1 Molar measurements by sex

| SEX | | AUM1W | AUM1L | AUM2W | AUM2L | ALM1W | ALM1L | ALM2W | ALM2L |
|---|---|---|---|---|---|---|---|---|---|
| . | 0.39 | 0.343333 | 0.424167 | 0.3225 | 0.24 | 0.329583 | 0.261364 | 0.335 | 0.3364 |
| | N | 12 | 12 | 12 | 12 | 12 | 12 | 11 | 11 |
| | Std. Deviation | 0.035866 | 0.018007 | 0.050625 | 0.035452 | 0.039254 | 0.032225 | 0.038477 | 0.030984 |
| female | Mean | 0.386277 | 0.338163 | 0.415109 | 0.3225 | 0.231979 | 0.31875 | 0.255745 | 0.329681 |
| | N | 47 | 49 | 46 | 46 | 48 | 48 | 47 | 47 |
| | Std. Deviation | 0.046291 | 0.028334 | 0.054554 | 0.037398 | 0.042536 | 0.037424 | 0.046892 | 0.037769 |
| male | Mean | 0.394417 | 0.346471 | 0.414643 | 0.323036 | 0.245656 | 0.327583 | 0.269153 | 0.332069 |
| | N | 60 | 68 | 56 | 56 | 61 | 60 | 59 | 58 |
| | Std. Deviation | 0.053845 | 0.033835 | 0.059642 | 0.043272 | 0.048395 | 0.034278 | 0.052965 | 0.031373 |
| r-value | | 0.16191 | **0.49569**** | **0.30004*** | **0.44379***** | -0.12268 | 0.23533 | 0.12291 | **0.43536***** |
| p-value | | 0.2937 | **0.01616**** | **0.05997*** | **0.00526***** | 0.43894 | 0.14379 | 0.44392 | **0.00561***** |
| Total | Mean | 0.390756 | 0.343023 | 0.415833 | 0.322763 | 0.239669 | 0.32425 | 0.263034 | 0.331379 |
| | N | 119 | 129 | 114 | 114 | 121 | 120 | 117 | 116 |
| | Std. Deviation | 0.049191 | 0.030717 | 0.056341 | 0.039884 | 0.045418 | 0.035389 | 0.049428 | 0.033832 |

*=significant at 0.1 level **=significant at 0.05 level ***=significant at 0.001 level

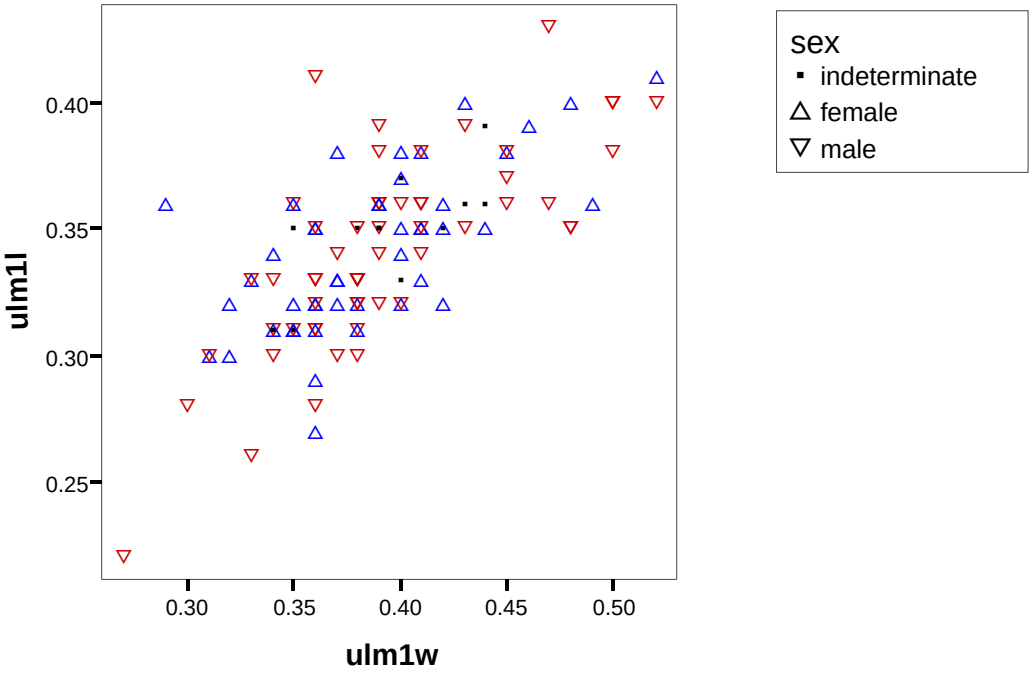


**Figure 11 Left upper 1st molar size by sex**

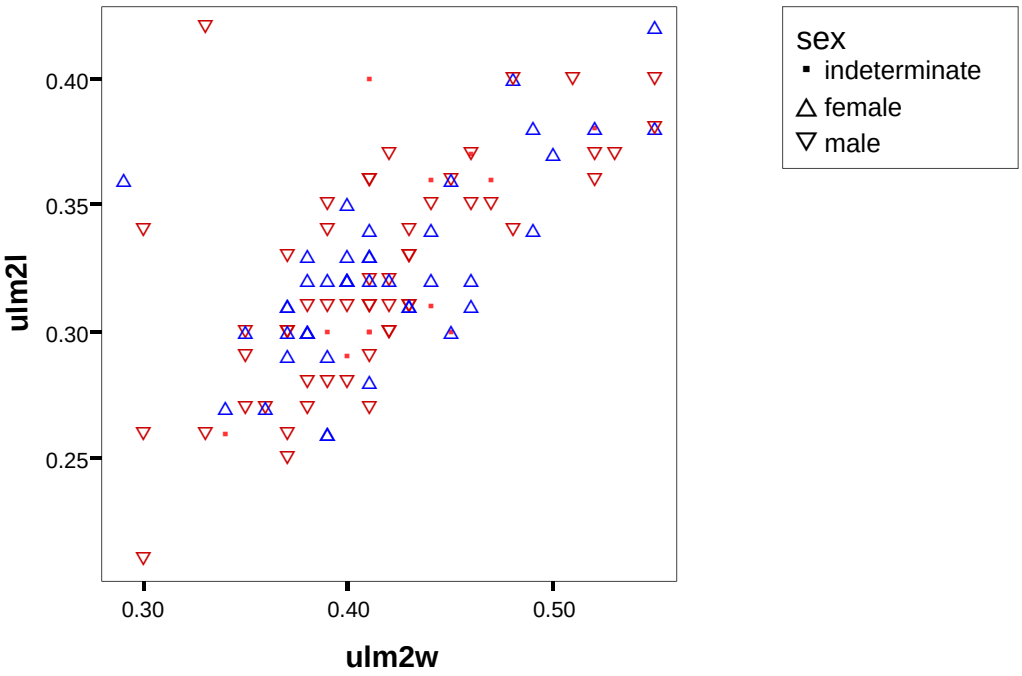


**Figure 12 Left upper 2nd molar size by sex**

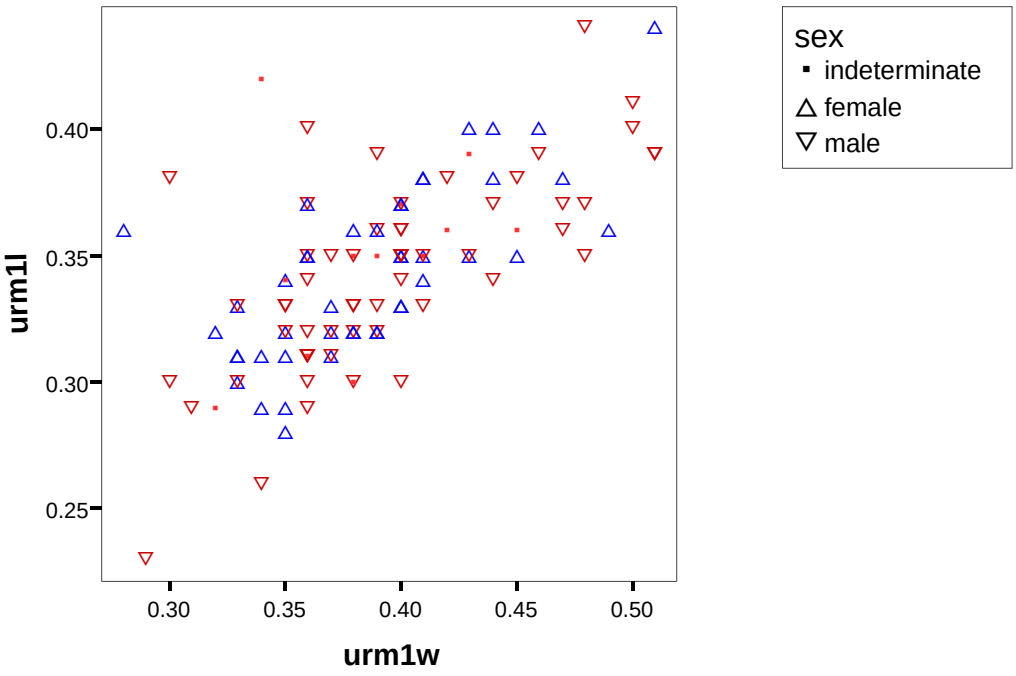


**Figure 13 Right upper 1st molar size by sex**

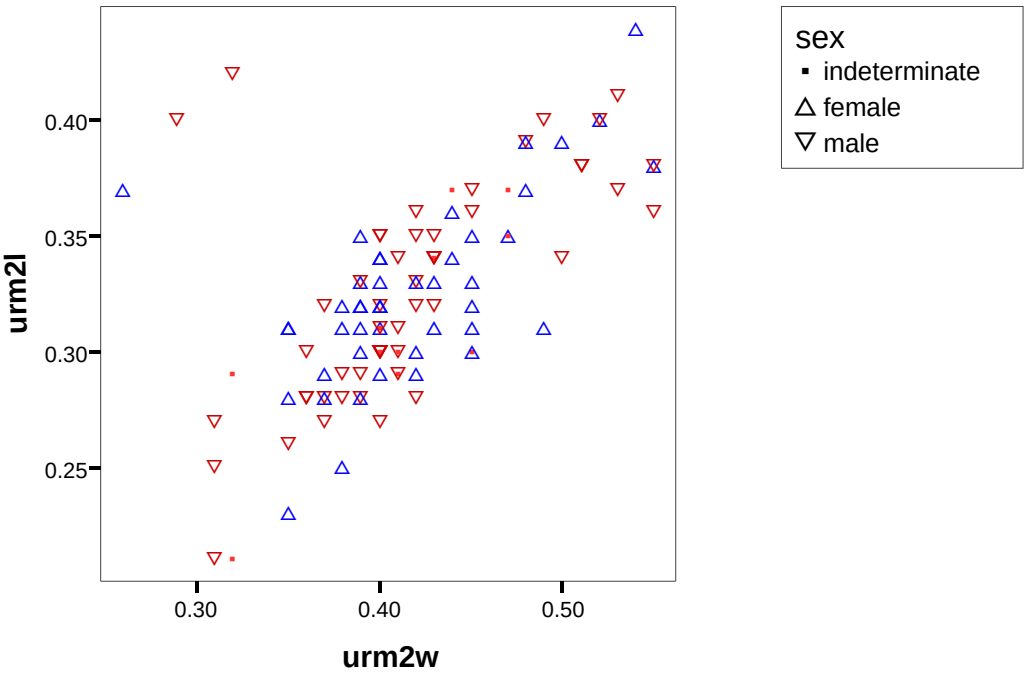


**Figure 14 Right upper 2nd molar size by sex**

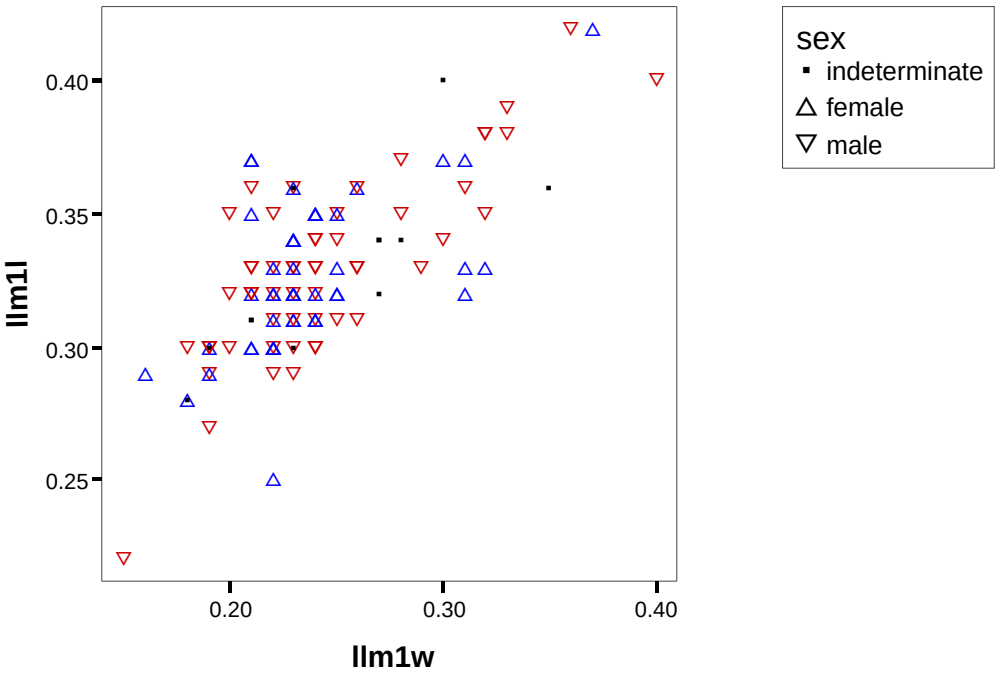


**Figure 15 Left lower 1st molar size by sex**

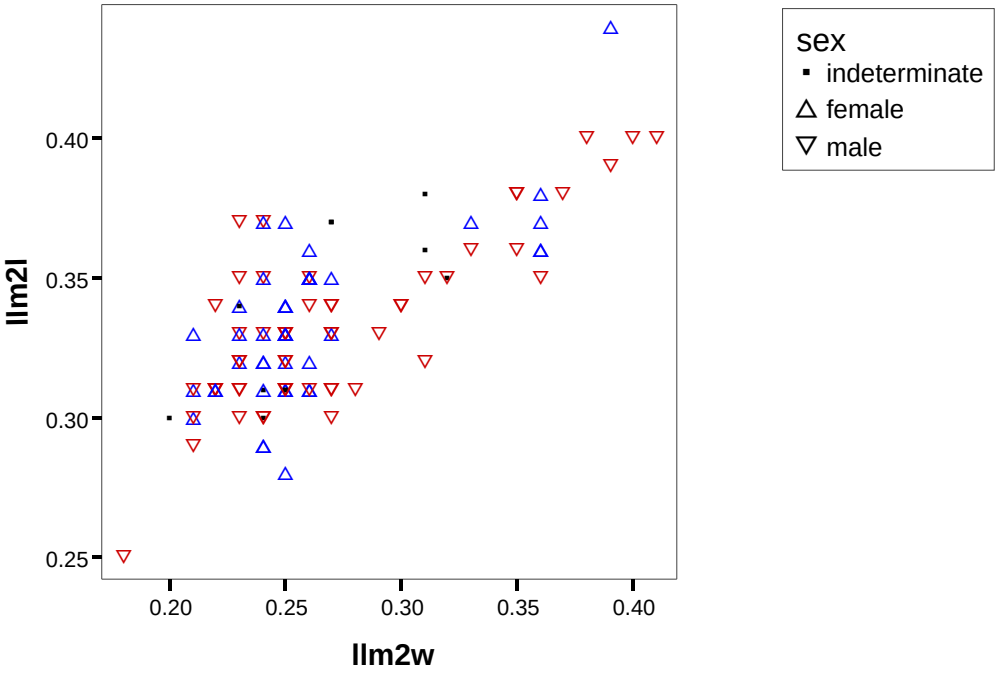


**Figure 16 Left lower 2nd molar size by sex**

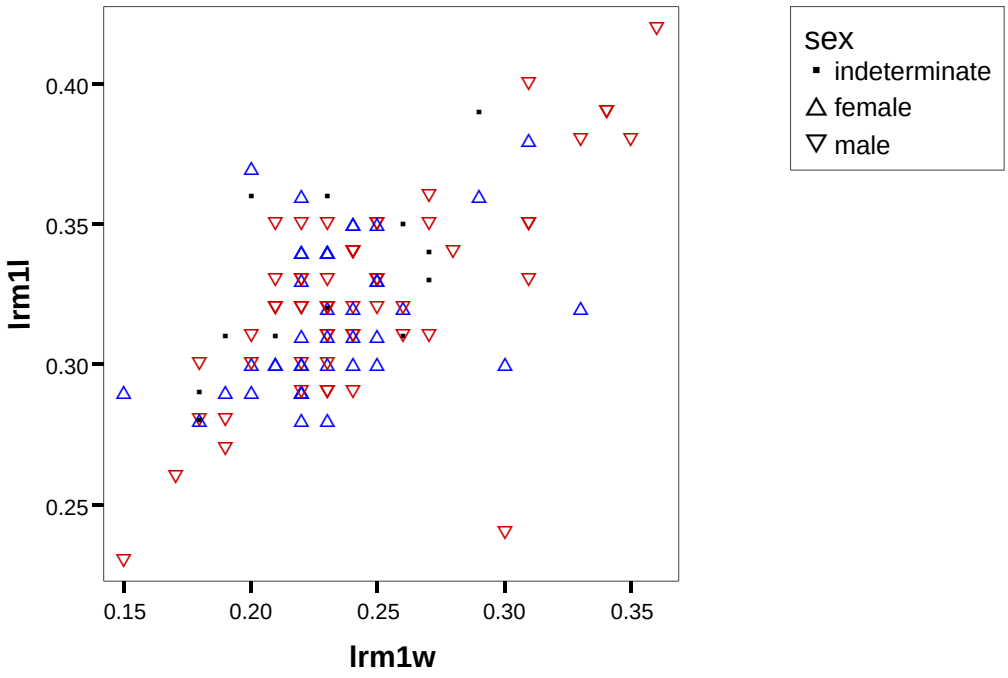


**Figure 17 Right lower 1st molar size by sex**

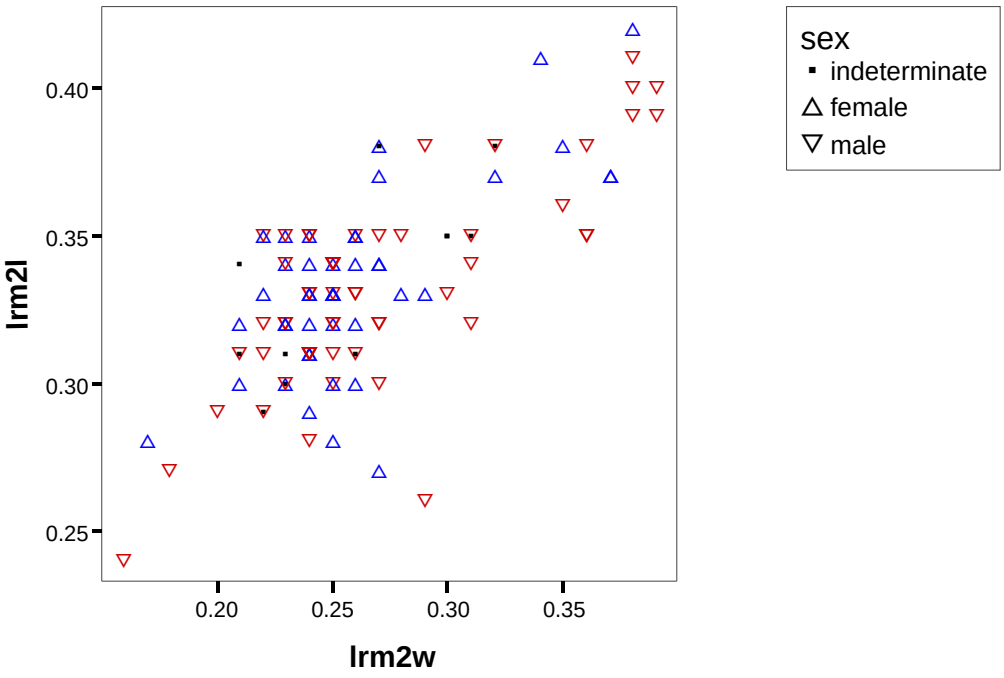


**Figure 18 Right lower second molar size by sex**

### 4.2.2. View of the Data by Attributed Taxonomic Label

There were noticeable differences in tooth measurements by received taxonomic labels. The relevance of noting this fact is that it is possible to suggest that these differences support the current three subspecies arrangement. At the very least, the current taxonomic assignments follow the expected arrangement of *P. p. edwardsi* having the largest cheek teeth.

Table 2 Molar measurements by subspecies as labeled in museums (in cm)

| SSP | | AUM1W | AUM1L | AUM2W | AUM2L | ALM1W | ALM1L | ALM2L | ALM2W |
|---|---|---|---|---|---|---|---|---|---|
| . | Mean | 0.394444 | 0.3485 | 0.411765 | 0.322059 | 0.24275 | 0.33 | 0.261842 | 0.339474 |
| | N | 18 | 20 | 17 | 17 | 20 | 20 | 19 | 19 |
| | Std. Deviation | 0.042423 | 0.028382 | 0.050743 | 0.041984 | 0.050406 | 0.032404 | 0.039798 | 0.027883 |
| *edwardsi* | Mean | 0.46225 | 0.371818 | 0.499211 | 0.369211 | 0.307895 | 0.360263 | 0.349167 | 0.375278 |
| | N | 20 | 22 | 19 | 19 | 19 | 19 | 18 | 18 |
| | Std. Deviation | 0.042965 | 0.022706 | 0.045925 | 0.031853 | 0.03698 | 0.034499 | 0.042087 | 0.024762 |
| *ibeanus* | Mean | 0.367833 | 0.322344 | 0.401786 | 0.304286 | 0.215167 | 0.300833 | 0.243571 | 0.313036 |
| | N | 30 | 32 | 28 | 28 | 30 | 30 | 28 | 28 |
| | Std. Deviation | 0.03525 | 0.029973 | 0.035984 | 0.033214 | 0.034553 | 0.037488 | 0.035846 | 0.037721 |
| *potto* | Mean | 0.374902 | 0.341545 | 0.3934 | 0.3157 | 0.227692 | 0.322353 | 0.244135 | 0.322941 |
| | N | 51 | 55 | 50 | 50 | 52 | 51 | 52 | 51 |
| | Std. Deviation | 0.032488 | 0.025145 | 0.040789 | 0.032087 | 0.022545 | 0.022346 | 0.023152 | 0.019904 |
| *potto* x *ibeanus* | r-value | 0.24974 | 0.1469 | 0.03636 | -0.25979 | **0.43539**** | 0.22226 | -0.01127 | 0.01445 |
| | p-value | 0.20901 | 0.43035 | 0.86606 | 0.22023 | **0.01618** | 0.23782 | 0.95286 | 0.93958 |
| *potto* x *edwardsi* | r-value | -0.18397 | -0.11231 | 0.04305 | -0.27651 | -0.34315 | -0.24611 | **-0.4971**** | 0.04954 |
| | p-value | 0.46493 | 0.62788 | 0.87423 | 0.29987 | 0.15034 | 0.30979 | **0.03582**** | 0.84523 |
| *ibeanus* x *edwardsi* | r-value | -0.24234 | **-0.3905*** | 0.03636 | -0.25979 | **0.43539**** | 0.22226 | -0.01127 | 0.01445 |
| | p-value | 0.3326 | **0.0723*** | 0.86606 | 0.22023 | **0.01618**** | 0.23782 | 0.95286 | 0.93958 |
| Total | Mean | 0.390756 | 0.343023 | 0.415833 | 0.322763 | 0.239669 | 0.32425 | 0.263034 | 0.331379 |
| | N | 119 | 129 | 114 | 114 | 121 | 120 | 117 | 116 |
| | Std. Deviation | 0.049191 | 0.030717 | 0.056341 | 0.039884 | 0.045418 | 0.035389 | 0.049428 | 0.033832 |

*=significant at 0.1 level **=significant at 0.05 level ***=significant at 0.001 level

Looking at the difference in molar size by cranial length indicates the presence of a distinct cluster of individuals:

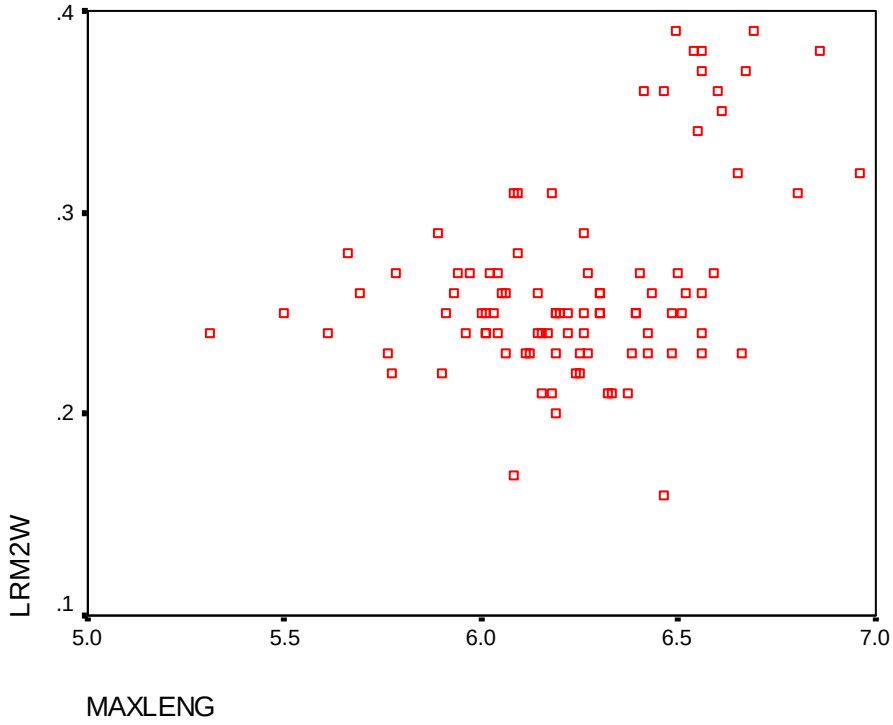


**Figure 19 Width of lower right 2nd molar by maximum cranial length**

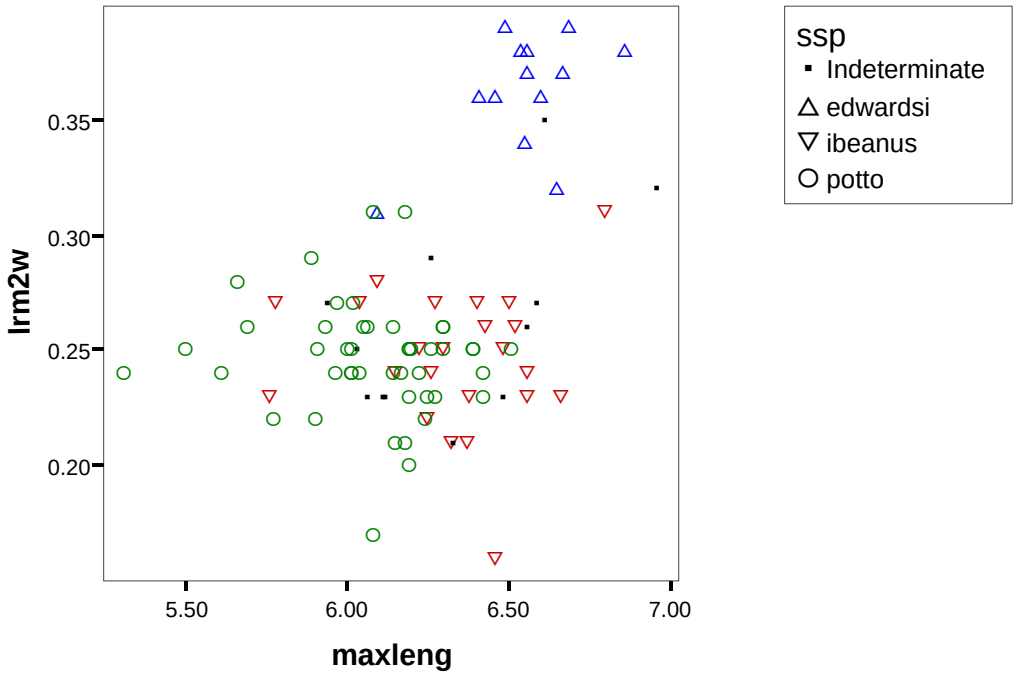


**Figure 20 Width of lower right 2nd molar by maximum cranial length labeled by assigned taxonomy**

This corresponds to the previously labeled taxonomy identifying *P. p. edwardsi* as having substantially larger cheek teeth. Also, it tends to be the width of the molars rather than the length of the molars which separates out *P. p. edwardsi*:

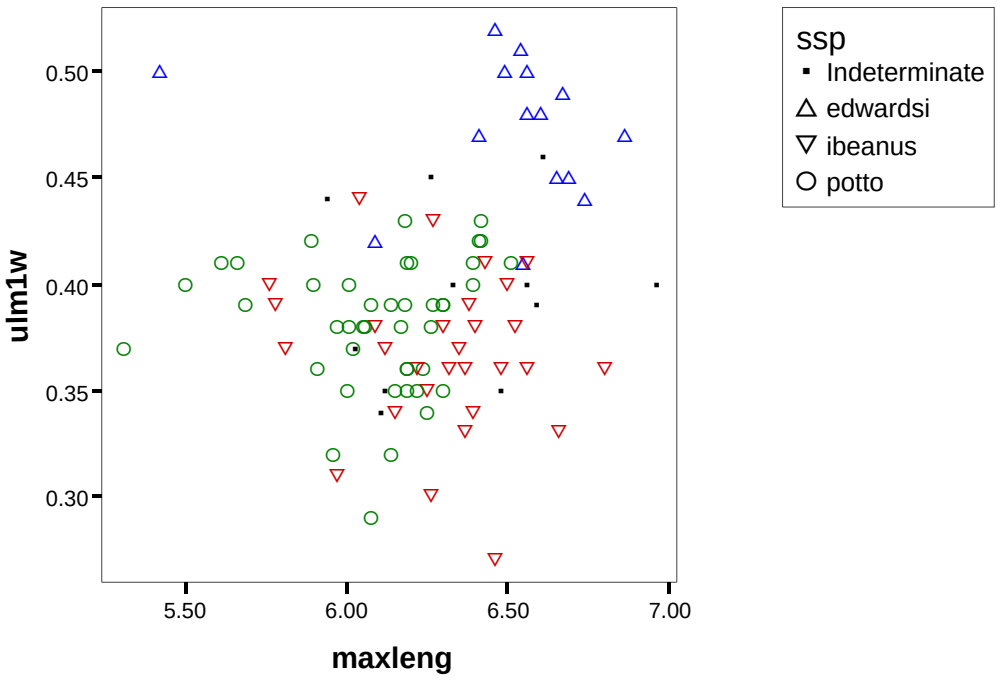


**Figure 21 Molar width of upper left 1st molar by maximum cranial length**

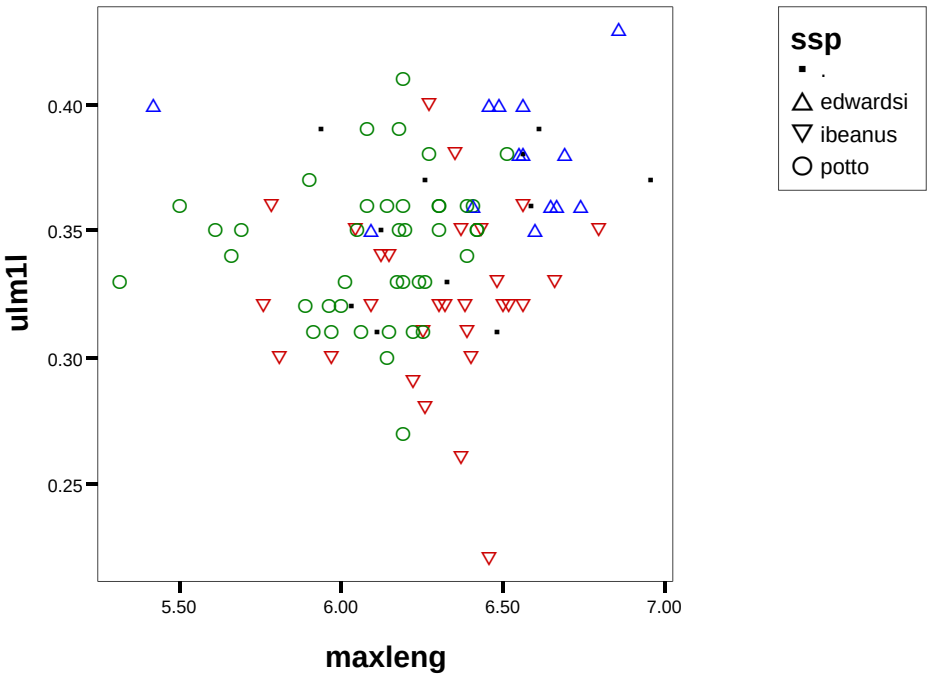


**Figure 22 Molar length of upper 1st molar by maximum cranial length**

When viewed by the dimensions of both molar width and length the label *P. p. edwardsi* still stands out:

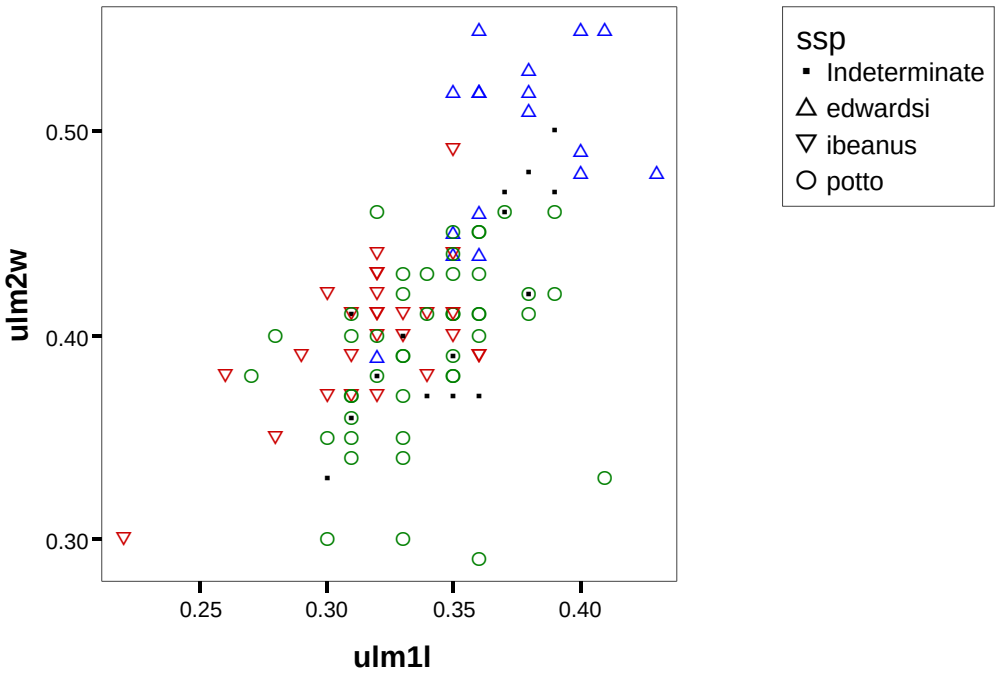


**Figure 23 Molar size (width x length) by assigned label**

In addition, specimens from the localities reported for *P. p. edwardsi* who had the expected large molar size values were examined separately by maximum cranial length to determine in a large-tooth/small-skull form could be identified as per the traditional taxonomic descriptions distinguishing *P. p. edwardsi* from *P. p. faustus*. With the exception of an odd outlier at 5.42 cm, only one specimen, AMNH 54340 from the Swanke region of the Congo, recorded as 6.09 cm, was found in the large molar forms which had a maximum cranial length size in the expected range for *P. p. faustus.*

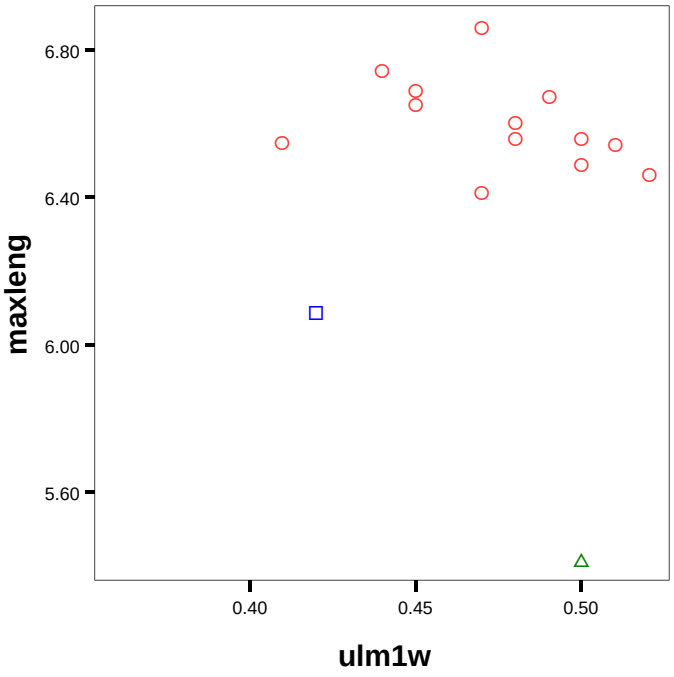


**Figure 24 Maximum cranial length versus tooth width in specimens labeled *P. p. edwardsi***

Hence there was exactly one specimen that conformed to the expectations for the identification of *P. p. faustus*, and another (located at the bottom of the graph) which was significantly smaller than expectations even for *P. p. faustus*. It is possible this specimen is actually a mislabeled *P. p. ibeanus* because some specimens of *P. p. ibeanus* at the AMNH has been previously been labeled as *P. p. faustus;* hence the comparison was expanded to include those specimens as well.

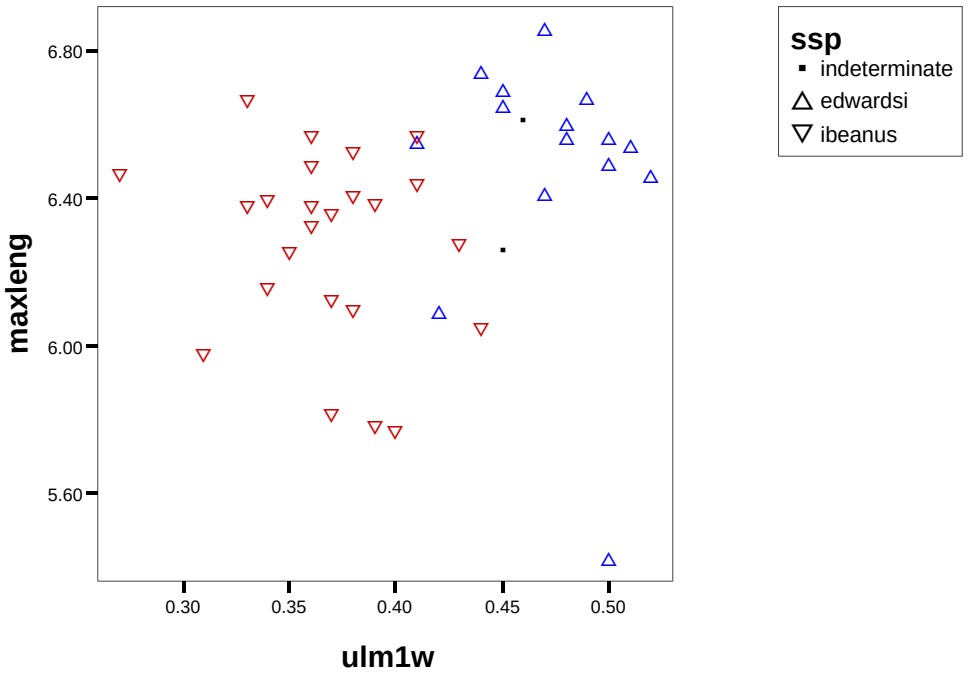


**Figure 25 Maximum cranial length x molar width for specimens labeled *edwardsi* or previously labeled *faustus* now labeled as *ibeanus***

Rather than revealing large-toothed specimens with smaller skulls versus large-toothed specimens with bigger skulls, the plot confirms the distinction large and smaller-toothed specimens.

In addition, some specimens labeled as *P. p. potto* from the regions around Dahomey and Nigeria were identified, based on pelage and tail length, as potential members of a taxon corresponding to the description of *P. p. ju-ju*. *P. p. ju-ju* was described dentally as having smaller teeth than *P. p. potto*. The cases which may represent *P. p. ju-ju* were relabeled and the graph was re-plotted with the rest of the specimens labeled as *P. p. potto*.

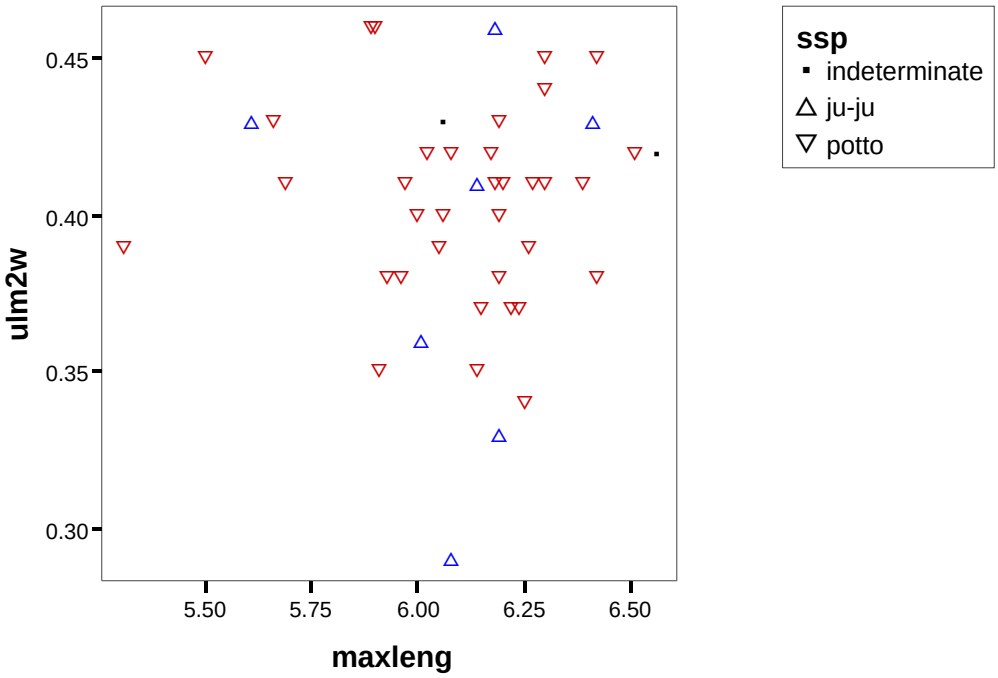


**Figure 26 Maximum cranial length x molar width in specimens which may be *P. p. ju-ju* and those resembling *P. p. potto***

No difference in the distribution of values was found for any of the dental measurements for those specimens provisionally associated with the taxa *P. p. ju-ju* and *P. p. potto* (see Figure 22).

## 4.3. Summary

The expectation from the received taxonomies is that *P. p. edwardsi* should have the largest cheek teeth while *P. p. ju-ju*, *P. p. ibeanus*, and *P. p. potto* are supposed to have the smallest teeth. *P. p. ibeanus* is supposed to have $M^2$ smaller than $M^1$ while *P. p. ju-ju* is supposed to have

$M^2$ and $M^1$ of approximately the same size. *P. p. potto* is also supposed to be distinguished by a tiny anterior lower premolar.

Those specimens labeled as *P. p. edwardsi* clearly had the largest teeth in both the length and width of the first two upper and lower molars. The specimens labeled as *P. p. ibeanus* and *P. p. potto*, including potential representatives of *P. p. faustus* and *P. p. ju-ju*, had much smaller teeth.

**Table 3 Molar measurements by previously assigned taxonomic labels (in cm)**

| SSP | AUM1W | AUM1L | AUM2W | AUM2L | ALM1W | ALM1L | ALM2W | ALM2L |
|---|---|---|---|---|---|---|---|---|
| *edwardsi* | 0.47 | 0.38 | 0.50 | 0.37 | 0.31 | 0.36 | 0.35 | 0.38 |
| *ibeanus* | 0.37 | 0.32 | 0.40 | 0.31 | 0.22 | 0.30 | 0.25 | 0.32 |
| *potto* | 0.38 | 0.34 | 0.40 | 0.32 | 0.23 | 0.32 | 0.25 | 0.32 |

It is revealing to also look at the same measurements by region. The specimens from Cameroon by far had the largest teeth, with those from Equatorial Guinea (French Equatorial Africa) and Gabon having the next largest molar sizes. These regions all occur in the central part of the potto range, the area predominantly associated with *P. p. edwardsi*. Specimens from Congo and the Central African Republic are also from the central zone and also had large values for the molars, especially the width of $M^2$. Specimens from Nigeria also had a fairly wide $M^2$ and that region is relatively close to the aforementioned group of countries. Specimens from Ghana, Ivory Coast, Dahomey (western range) and Kenya (eastern range), and the DRC (central range), on the other hand, tended to have notably small values for the length and width of their molars.

**Table 4 Molar measurements by country (in cm)**

| Country | AUM1W | AUM1L | AUM2W | AUM2L | ALM1W | ALM1L | ALM2W | ALM2L |
|---|---|---|---|---|---|---|---|---|
| Cameroon | 0.48 | 0.38 | 0.51 | 0.38 | 0.32 | 0.37 | 0.36 | 0.38 |
| CAR | 0.42 | 0.36 | 0.44 | 0.36 | 0.26 | 0.34 | 0.29 | 0.36 |
| Congo | 0.42 | 0.35 | 0.45 | 0.30 | 0.27 | 0.32 | 0.31 | 0.36 |
| Dahomey | 0.36 | 0.35 | 0.32 | 0.33 | 0.21 | 0.33 | 0.22 | 0.32 |
| Fren Eq | 0.44 | 0.36 | 0.48 | 0.36 | 0.29 | 0.37 | 0.29 | 0.36 |
| Gabon | 0.41 | 0.37 | 0.48 | 0.38 | 0.29 | 0.33 | 0.33 | 0.38 |
| Ghana | 0.35 | 0.32 | 0.36 | 0.29 | 0.22 | 0.31 | 0.24 | 0.32 |
| Ivory Co | 0.38 | 0.34 | 0.41 | 0.32 | 0.24 | 0.32 | 0.25 | 0.32 |
| Kenya | 0.38 | 0.31 | 0.39 | 0.28 | 0.25 | 0.30 | 0.27 | 0.31 |
| Liberia | 0.39 | 0.35 | 0.42 | 0.32 | 0.23 | 0.34 | 0.25 | 0.34 |
| Nigeria | 0.40 | 0.37 | 0.41 | 0.36 | 0.23 | 0.33 | 0.26 | 0.33 |
| Uganda | 0.36 | 0.33 | 0.41 | 0.31 | 0.23 | 0.31 | 0.27 | 0.32 |
| Zaire | 0.37 | 0.33 | 0.41 | 0.31 | 0.21 | 0.30 | 0.24 | 0.33 |

The specimens labeled as *P. p. ibeanus* as well as specimens identified only as being from Kenya and Uganda, the range of *P. p. ibeanus*, have $M^2$ length shorter than $M^1$ length but $M^1$ is wider than $M^2$. Whether this result will be reliable with a greater sample size and what meaning this might have is unclear.

The western range of the genus is associated with *P. p. potto*. Specimens from the western range of *Perodicticus*, especially those from Ghana and the Ivory Coast, do frequently have a small middle (lower and sometimes upper) premolar. Ivory Coast and Ghana also happened to have

some of the smallest overall molar sizes. Also predominantly in the western part of the pottos' range is a new feature—a bowed mesial edge shaped to varying degrees like a fin on the lower anterior (caniniform) premolar.

The stepwise pattern of the upper canine-premolar series versus the non-stepwise pattern identified by Schwartz and Beutel (1995) was confirmed throughout the range of *Perodicticus*.

## 4.4. Conclusions

Overall, the following dental diagnostic traits for potential morphs could be identified:

- The presence or absence of a stepwise pattern of the upper canine-premolar series versus a non-stepwise pattern, identified by Schwartz and Beutel (1995)
- The presence or absence of a tiny middle lower and upper middle premolar
- The presence or absence of relatively large cheek teeth, especially the width of the molars
- The presence or absence of a bowed fin on the mesial keel of the lower anterior caniniform premolars

- The stepwise pattern (or lack thereof), the diminutive middle anterior (upper or lower) premolar, and the bowed fin on the lower anterior premolars are not mutually exclusive traits.

# 5. CRANIUM

## 5.1. Non-Metric Data

There were no readily apparent differences between the appearances of the skulls studied from the range of the genus *Perodicticus*. While such traits may in fact exist, the most readily accessible cranial differences are best characterized and summarized through metric analysis, which follows below.

## 5.2. Metric Data

### 5.2.1. View of the Data by Sex

Pooling the entire sample from the entire range, there was moderate sexual dimorphism in length of the nasal bones and the separation of the temporal lines, but not in the overall size of the skulls (measurements in cm).

Table 5 Cranial measurements by sex (in cm)

| SEX | | MAXLENG | MAXWIDTH | NASAL | MINTEMP |
|---|---|---|---|---|---|
| . | Mean | 6.255 | 4.5775 | 1.518333 | 1.364 |
| | N | 10 | 8 | 12 | 10 |
| | Std. Deviation | 0.3662801 | 0.21783021 | 0.157355 | 0.184884 |
| female | Mean | 6.1959524 | 4.43755556 | 1.585652 | 1.296667 |
| | N | 42 | 45 | 46 | 45 |
| | Std. Deviation | 0.2752831 | 0.30012994 | 0.13843 | 0.313767 |
| male | Mean | 6.2775439 | 4.51915254 | 1.544762 | 1.376066 |
| | N | 57 | 59 | 63 | 61 |
| | r-value | -0.02681 | 0.01349 | **0.26851*** | **0.29743*** |
| | p-value | 0.87666 | 0.93594 | **0.08169*** | **0.05895*** |
| | Std. Deviation | 0.3146783 | 0.32636603 | 0.150974 | 0.517237 |
| Total | Mean | 6.2440367 | 4.49053571 | 1.557686 | 1.344224 |
| | N | 109 | 112 | 121 | 116 |
| | Std. Deviation | 0.3046252 | 0.31060197 | 0.147562 | 0.425891 |

*=significant at 0.1 level **=significant at 0.05 level ***=significant at 0.001 level

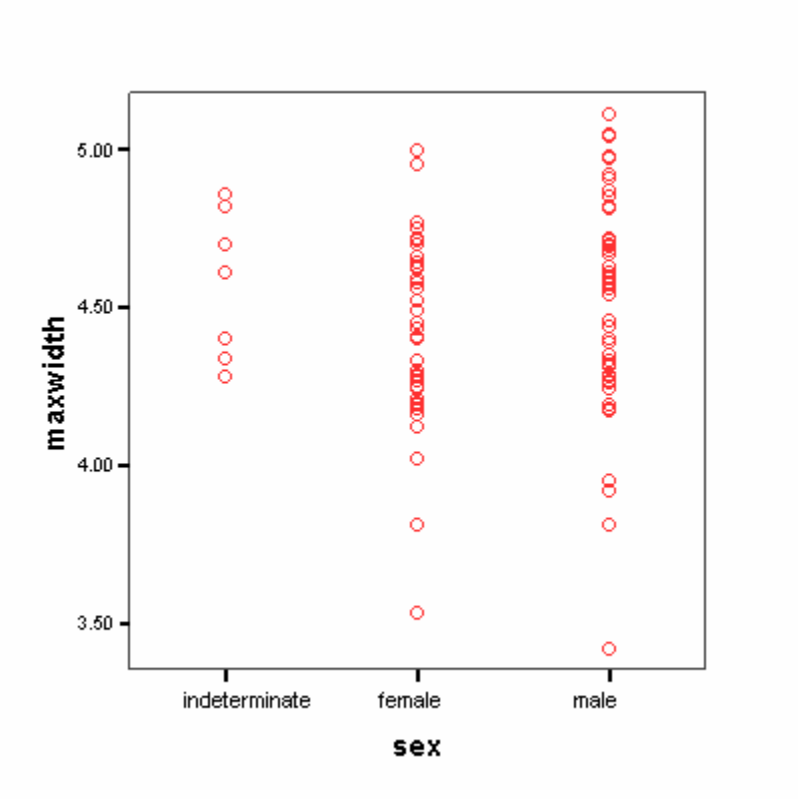


**Figure 27 Maximum skull width by sex**

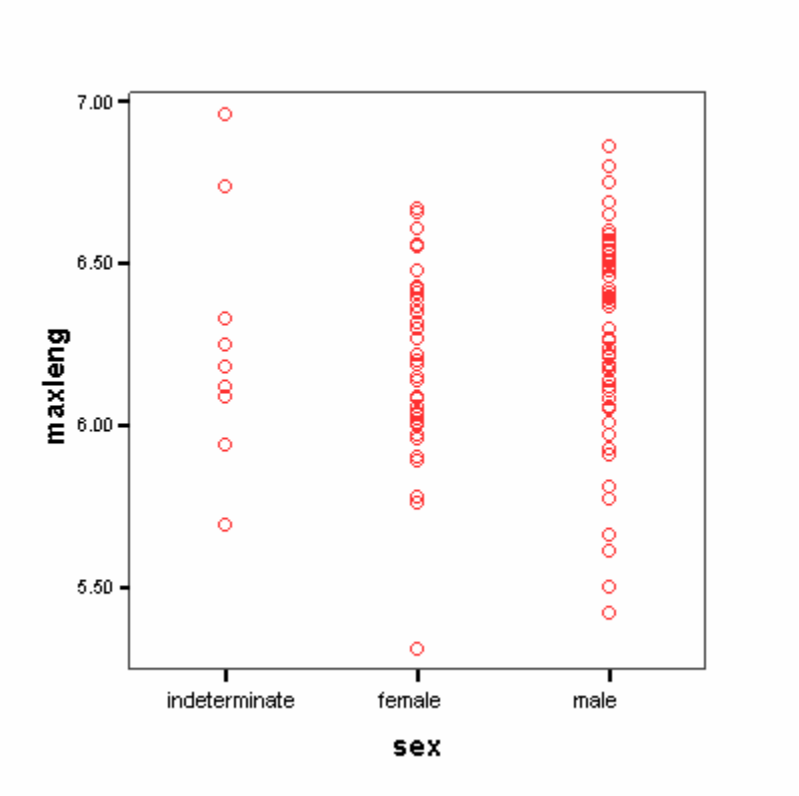


**Figure 28 Maximum skull length by sex**

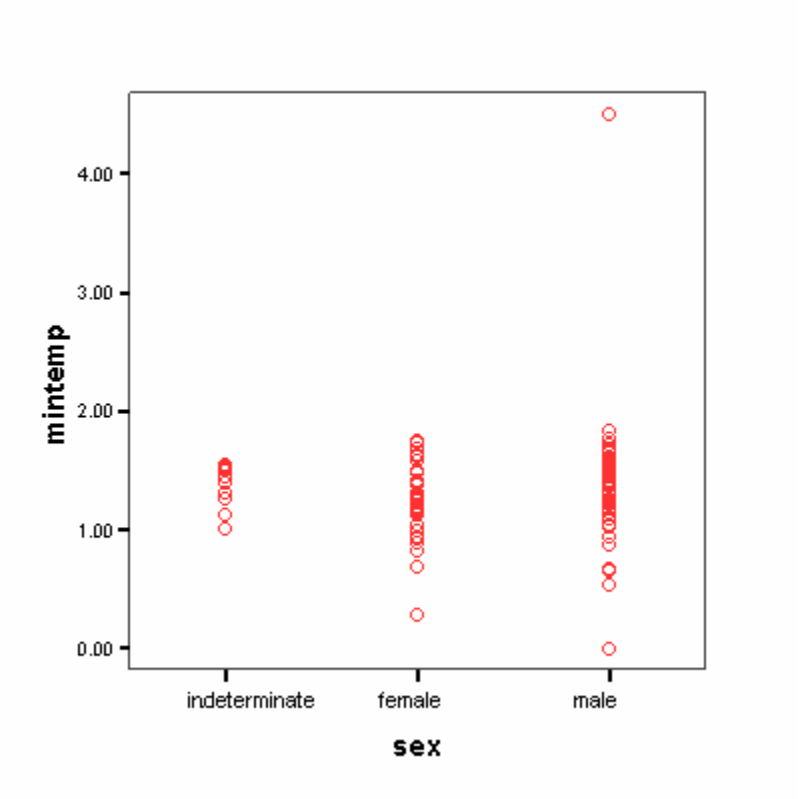


**Figure 29 Minimum temporal line separation by sex**

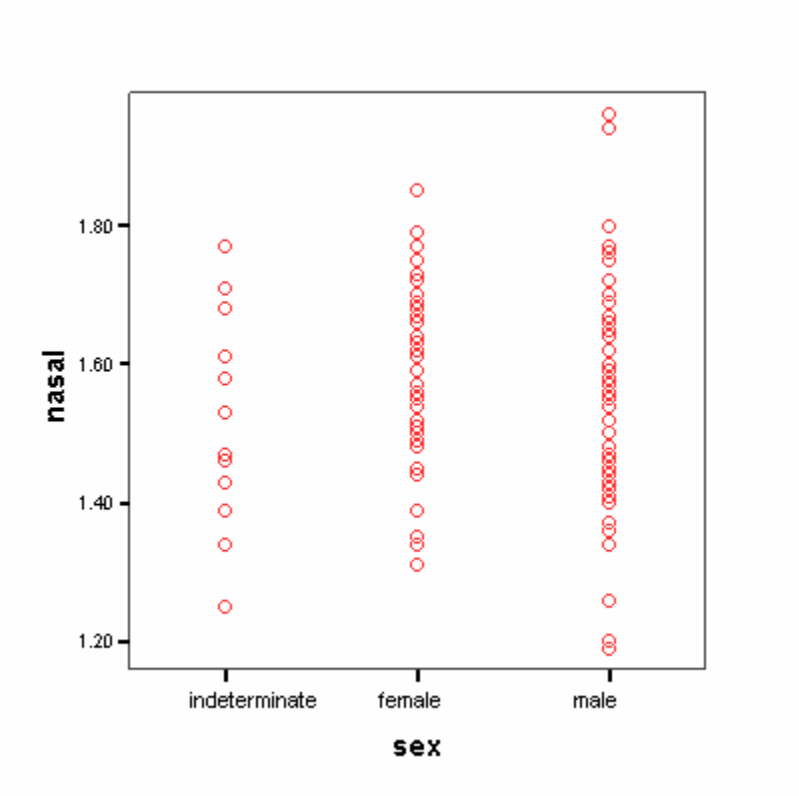


**Figure 30 Maximum nasal bone length by sex**

### 5.2.2. View of the Data by Attributed Taxonomic Label

Simply using the taxonomy previously assigned to the specimens in the collection, the skull width and skull length separate out *P. p. ibeanus*, *P. p. edwardsi*, and *P. p. potto*. *P. p. edwardsi* have the largest skulls, *P. p. ibeanus* have the next largest skulls, and specimens of *P. p. potto* have the smallest skulls. There was no appreciable separation based on the minimum temporal line separation, and a mild difference in the length of the nasal bones.

Table 6 Cranial measurement by taxonomic labels assigned by museums (in cm)

| SSP | | MAXLENG | MAXWIDTH | NASAL | MINTEMP |
|---|---|---|---|---|---|
| . | Mean | 6.369231 | 4.560625 | 1.564667 | 1.33625 |
| | N | 13 | 16 | 15 | 16 |
| | Std. Deviation | 0.314522 | 0.2691584 | 0.169067 | 0.357564 |
| edwardsi | Mean | 6.49125 | 4.7783333 | 1.640455 | 1.311111 |
| | N | 16 | 18 | 22 | 18 |
| | Std. Deviation | 0.331056 | 0.2867926 | 0.147954 | 0.407444 |
| ibeanus | Mean | 6.302188 | 4.5758621 | 1.508182 | 1.551875 |
| | N | 32 | 29 | 33 | 32 |
| | Std. Deviation | 0.246062 | 0.2567728 | 0.153041 | 0.559299 |
| potto | Mean | 6.088958 | 4.3114286 | 1.551961 | 1.2258 |
| | N | 48 | 49 | 51 | 50 |
| | Std. Deviation | 0.247104 | 0.2510395 | 0.124065 | 0.296924 |
| *potto* x *ibeanus* | r-value | 0.06169 | -0.226 | 0.12468 | -0.17386 |
| | p-value | 0.75987 | 0.27735 | 0.50396 | 0.36707 |
| *potto* x *edwardsi* | r-value | 0.0732 | **-0.47294*** | **0.40449*** | 0.00988 |
| | p-value | 0.81214 | **0.07501*** | **0.06187*** | 0.96997 |
| *ibeanus* x *edwardsi* | r-value | -0.20745 | -0.28808 | -0.08355 | 0.28582 |
| | p-value | 0.44075 | 0.27926 | 0.71165 | 0.25025 |
| Total | Mean | 6.244037 | 4.4905357 | 1.557686 | 1.344224 |
| | N | 109 | 112 | 121 | 116 |
| | Std. Deviation | 0.304625 | 0.310602 | 0.147562 | 0.425891 |

*=significant at 0.1 level **=significant at 0.05 level ***=significant at 0.001 level

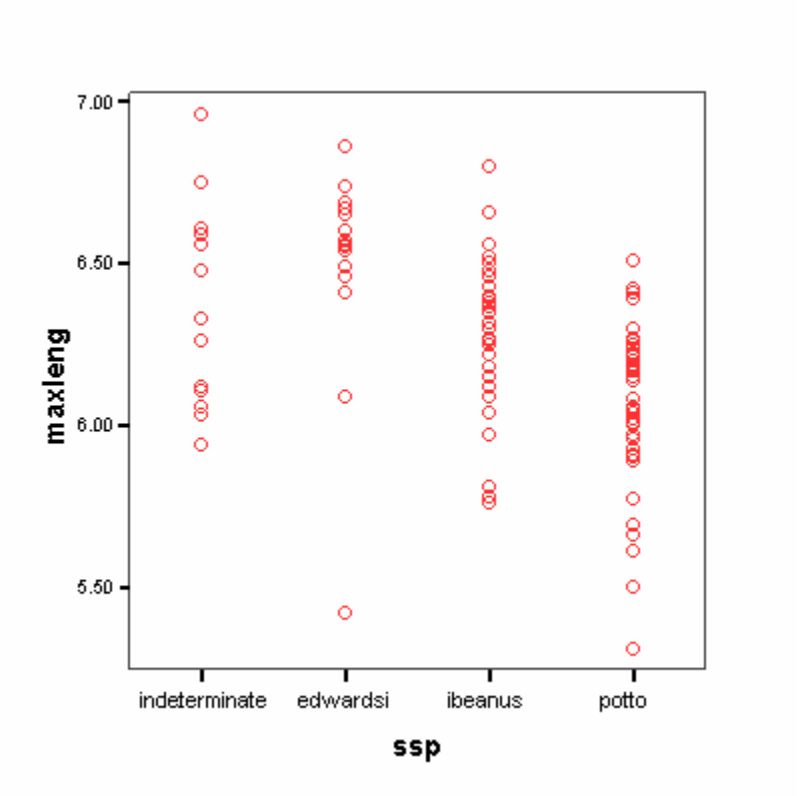


**Figure 31 Maximum skull length by museum assigned taxonomy**

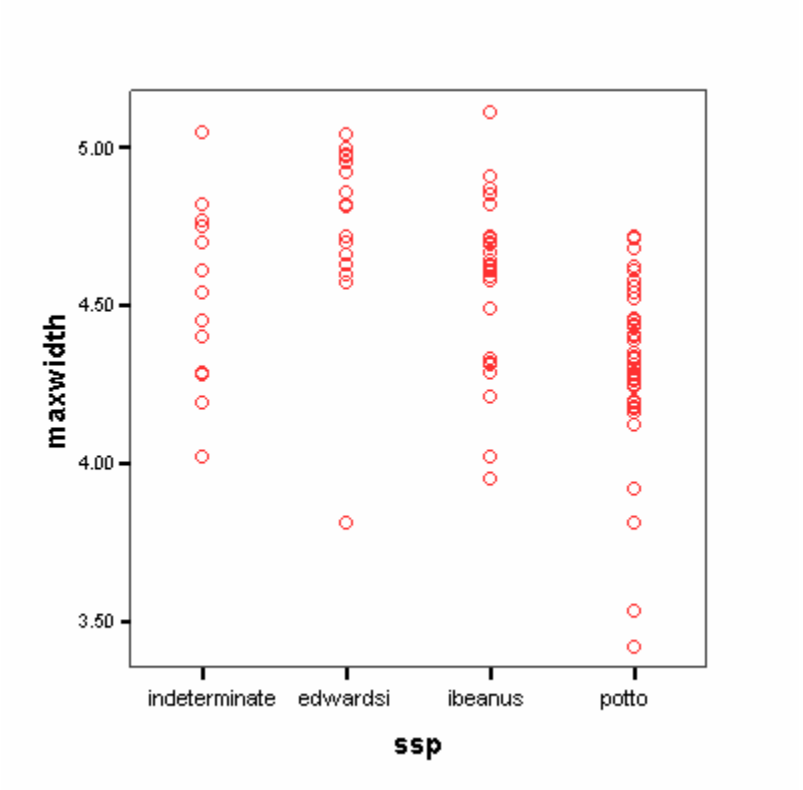


**Figure 32 Maximum skull width by museum assigned taxonomy**

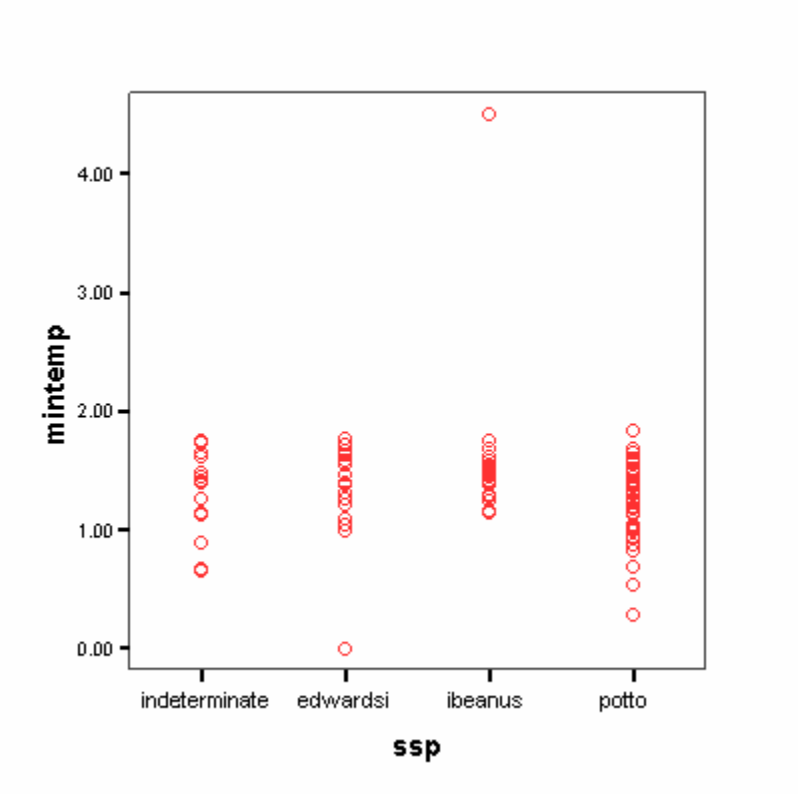


**Figure 33 Minimum temporal line separation by museum assigned taxonomy**

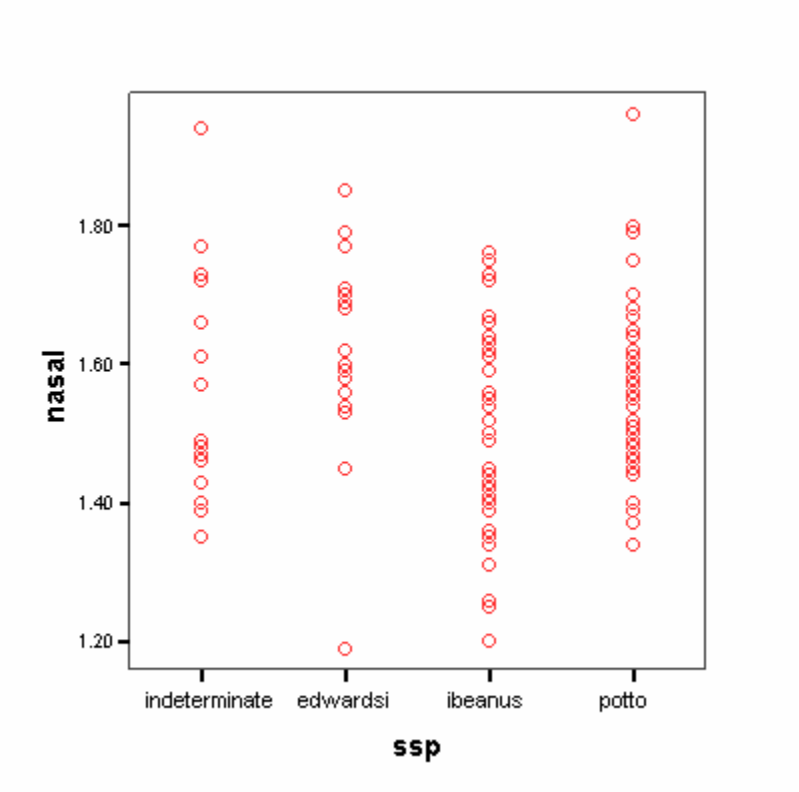


**Figure 34 Maximum nasal bone length by museum assigned taxonomy**

Based on the literature, specimens of *P. p. ju-ju* should have significantly larger skulls than specimens of *P. p. potto*. Specimens which have been tentatively identified as potential representatives of *P. p. ju-ju* based on pelage were compared to other specimens that conform to the standard description of *P. p. potto*. No difference in skull length was observed (Figure 27):

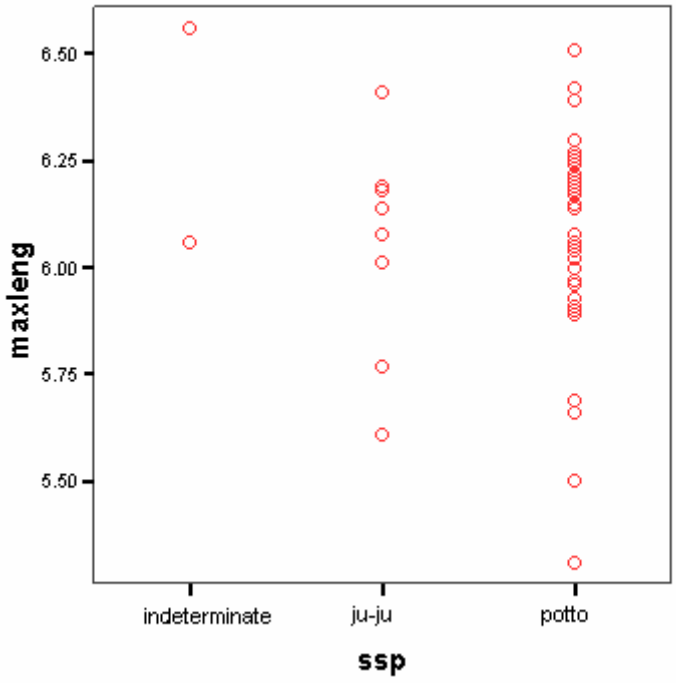


**Figure 35 Maximum cranial length--*potto* versus *ju-ju***

The mean for maximum cranial length was 6.04 cm (standard error .07) for *P. p. ju-ju* and 6.10 cm (standard error .04) for *P. p. potto*.

It is also informative to look at the measurements by location as a part of the assigned taxonomy.

**Table 7 Cranial measurements by country**

| COUNTRY | | MAXLENG | MAXWIDTH | NASAL | MINTEMP |
|---|---|---|---|---|---|
| . | Mean | 6.3683 | 4.5913 | 1.5675 | 1.2713 |
| | N | 6 | 8 | 8 | 8 |
| | Std. Deviation | 0.40226 | 0.23619 | 0.17019 | 0.32082 |
| Cameroon | Mean | 6.4858 | 4.7686 | 1.62 | 1.4077 |
| | N | 12 | 14 | 16 | 13 |
| | Std. Deviation | 0.35574 | 0.31574 | 0.16182 | 0.26537 |
| CAR | Mean | 6.4367 | 4.6186 | 1.575 | 1.3771 |
| | N | 6 | 7 | 6 | 7 |
| | Std. Deviation | 0.24394 | 0.27528 | 0.1692 | 0.62015 |
| Congo | Mean | 6.09 | | 1.53 | 1.39 |
| | N | 1 | | 1 | 1 |
| | Std. Deviation | . | | . | . |
| Dahomey | Mean | 5.976 | 4.2575 | 1.506 | 1.248 |
| | N | 5 | 4 | 5 | 5 |
| | Std. Deviation | 0.11908 | 0.09394 | 0.07925 | 0.16022 |
| Fren Eq | Mean | 6.74 | 4.82 | 1.695 | 1.55 |
| | N | 1 | 1 | 2 | 1 |
| | Std. Deviation | . | . | 0.02121 | . |
| Gabon | Mean | 6.55 | 4.93 | 1.78 | 1.18 |
| | N | 1 | 2 | 2 | 2 |
| | Std. Deviation | . | 0.09899 | 0.01414 | 0.19799 |
| Ghana | Mean | 6.065 | 4.34 | 1.5173 | 1.328 |
| | N | 8 | 10 | 11 | 10 |
| | Std. Deviation | 0.14412 | 0.1278 | 0.08855 | 0.17216 |
| Ivory Co | Mean | 6.1829 | 4.3365 | 1.5723 | 1.1555 |
| | N | 21 | 23 | 22 | 22 |
| | Std. Deviation | 0.22114 | 0.28142 | 0.13901 | 0.35558 |
| Kenya | Mean | 6.3 | 4.56 | 1.388 | 2.15 |
| | N | 4 | 4 | 5 | 5 |
| | Std. Deviation | 0.14236 | 0.22539 | 0.08983 | 1.31719 |
| Liberia | Mean | 6.0109 | 4.218 | 1.518 | 1.13 |
| | N | 11 | 10 | 10 | 10 |
| | Std. Deviation | 0.35189 | 0.30626 | 0.14085 | 0.3209 |
| Nigeria | Mean | 6.106 | 4.3475 | 1.666 | 1.324 |
| | N | 5 | 4 | 5 | 5 |
| | Std. Deviation | 0.2967 | 0.22618 | 0.10359 | 0.32539 |
| Uganda | Mean | 6.525 | 4.7 | 1.375 | 1.53 |
| | N | 2 | 1 | 2 | 1 |
| | Std. Deviation | 0.38891 | . | 0.17678 | . |
| Zaire | Mean | 6.2854 | 4.5733 | 1.5415 | 1.4377 |
| | N | 26 | 24 | 26 | 26 |
| | Std. Deviation | 0.24966 | 0.27003 | 0.14823 | 0.15863 |
| Total | Mean | 6.244 | 4.4905 | 1.5577 | 1.3442 |
| | N | 109 | 112 | 121 | 116 |
| | Std. Deviation | 0.30463 | 0.3106 | 0.14756 | 0.42589 |

The smaller values tend to come from specimens from the west in places like Dahomey, the Ivory Coast, and Ghana, while the highest values tend to come from the central part of the range, from specimens in places like Cameroon and Equatorial Guinea (French Eq). Since the general scheme for the received taxonomies is based on these geographic ranges the values by taxon concur with these values by region. The temporal line separation values are still consistently uniform, yet there is considerable more variation visible with the maximum length of the nasal bones. The specimens from the central region (Gabon, Cameroon, Equatorial Guinea) tend to have the longest nasal bones.

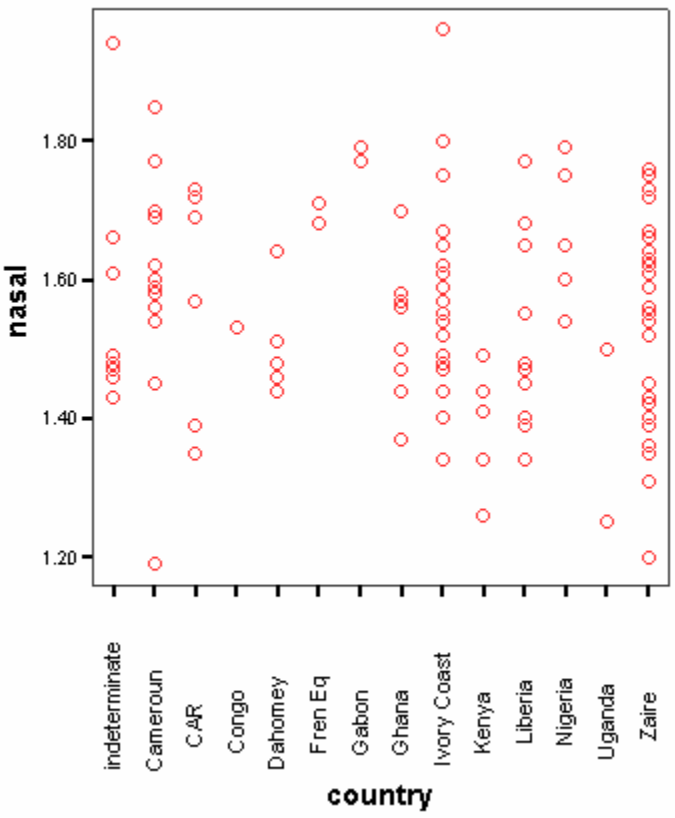


**Figure 36 Maximum nasal bone length by country**

## 5.3. Summary

The cranial length and width are consistently largest for those specimens labeled *P. p. edwardsi*, next largest for those labeled *P. p. ibeanus*, and the smallest values are found in those specimens labeled *P. p. potto*, consistent with received values.

**Table 8 Received values from the literature for maximum cranial length compared to study values**

| Ssp | Received Cranial Length | Study Cranial Length |
|---|---|---|
| *P. p. edwardsi* | 6.58 cm | 6.49 cm |
| *P. p. ibeanus* | 6.37 cm | 6.30 cm |
| *P. p. potto* | 6.14 cm | 6.09 cm |

The nasals were shorter for those specimens labeled as *P. p. ibeanus* than those listed for *P. p. potto* as expected, but not clear difference in the width of the skull (related to the width of the zygomatic arch) was detected.

The values for skulls size (maximum cranial length and width) were supposed to be largest for *P. p. edwardsi* and those specimens with the large molars from the designated localities of that taxon did indeed fulfill that expectation.

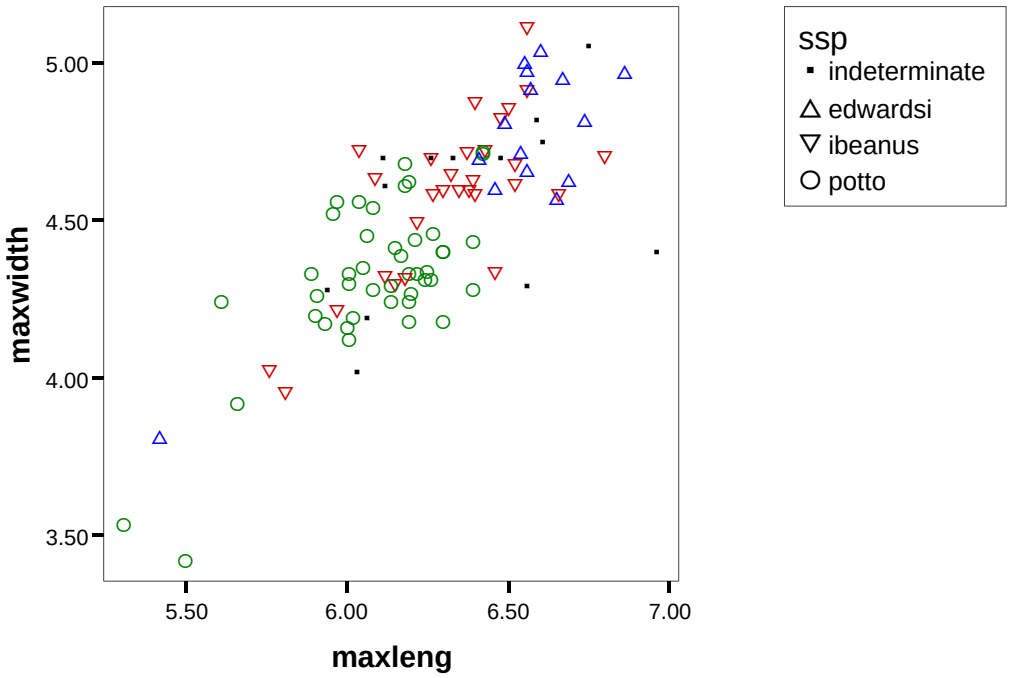


**Figure 37 Maximum cranial length versus width by museum assigned taxonomy**

## 5.4. Conclusion

Overall, the following cranial diagnostic traits for potential morphs could be identified:

- Differences in maximum cranial length
- Differences in maximum cranial width

# 6. POST CRANIUM

## 6.1. Non-Metric Data

There were surprising results for tail length. Specimens labeled as *P. p. ibeanus* from Kenya, which otherwise tend to match the descriptions for pelage markings and body size, have relatively short tails (Figure 40). Specimens of *P. potto* (often assigned as *P. p. potto*) from Dahomey, which may reflect a morph connected to the taxon *P. p. ju-ju*, have primarily short tails. Specimens of *P. potto potto* from Nigeria, which may also be a part of the morph connected to *P. p. ju-ju*, are split between short and medium tails. Specimens of *P. p. potto* from Ghana, Ivory Coast, and Liberia have predominantly long tails (Figures 38 and 39). Tail length is assigned as relative to whether the tail does not reach the ankles (short), only reaches the ankles (medium) or passes the ankles onto or beyond the hind foot (long).

**Figure 38 Example of long-tailed specimen from the western range of the genus**


**Figure 39 Another long-tailed potto. This specimen is from Ghana.**

**Figure 40 A short-tailed specimens listed as *P. p. ibeanus* from the eastern range of the genus**

## 6.2. Metric Data

### 6.2.1. View of the Data by Sex

There was little difference in tail length by sex, which conforms to the overall pattern of a lack of sexual dimorphism indicated in the measurements taken in this study. However, it is the largest amount of metrically observed sexual dimorphism in the study.

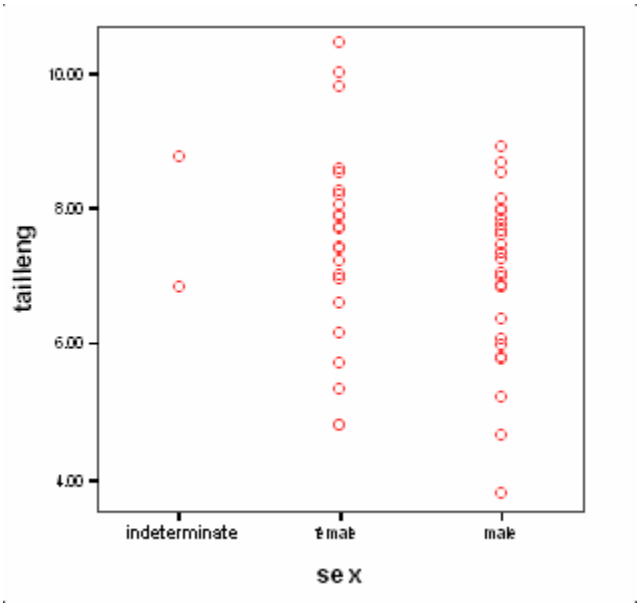


**Figure 41 Comparison of tail lengths of specimens attributed to *P. p. potto* by sex**

### 6.2.2. View of the Data by Attributed Taxonomic Label

A difference in tail length could be appreciated by measurement. However, notable differences by overall length from head to tail were not as apparent. The measurements supported the naked eye descriptions of differences in tail length by regions associated with various traditional taxa.

**Table 9 Mean tail length by country reflecting the differences by regions associated with different taxa with the longest and shortest observed tails**

| COUNTRY | Associated Taxon | Mean | N | Std. Deviation |
|---|---|---|---|---|
| Kenya | *P.p. ibeanus* | 5.388 | 5 | 1.80546 |
| Dahomey | *P. p. ju-ju* | 4.72 | 9 | 0.7881 |
| Nigeria | *P. p. ju-ju* | 6.4929 | 7 | 1.00109 |
| Liberia | *P. p. potto* | 7.4888 | 8 | 1.46801 |
| Ivory Co | *P. p. potto* | 7.5732 | 22 | 1.12915 |
| Ghana | *P. p. potto* | 7.7847 | 15 | 0.55681 |
| Total | | 6.9418 | 66 | 1.51886 |

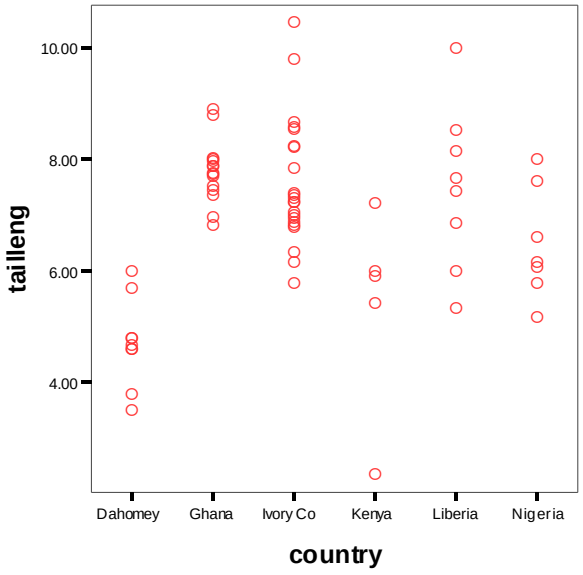


**Figure 42 Tail length by country--note how small specimens from Dahomey are compared to other areas**

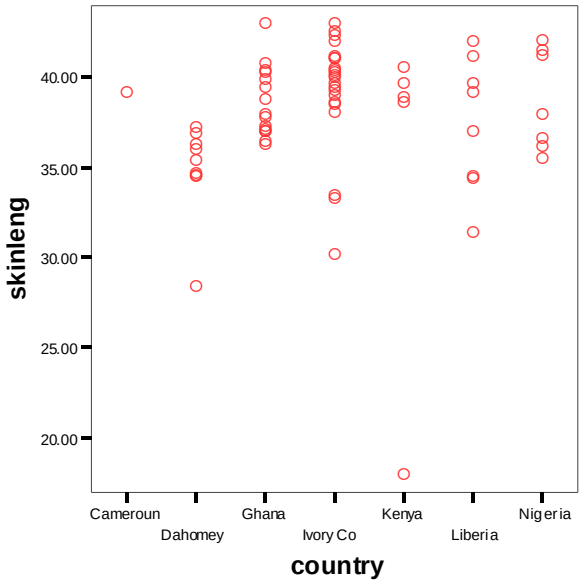


**Figure 43 Body (pelage) length by country--overall lengths tend to be more similar**

## 6.3. Summary

The observation that *P. p. ibeanus* has a "relatively" longer tail seems false if the basis for comparison is other pottos. If the distinct pelages of specimens from Dahomey and Nigeria do represent the old taxon *P. p. ju-ju* (see Chapter 7), then the claim that members of that taxon have longer tails also appears incorrect. It is in fact the specimens from the farthest portion of the western range, which have previously been identified as *P. p. potto*, which has the longest tails relative to other pottos.

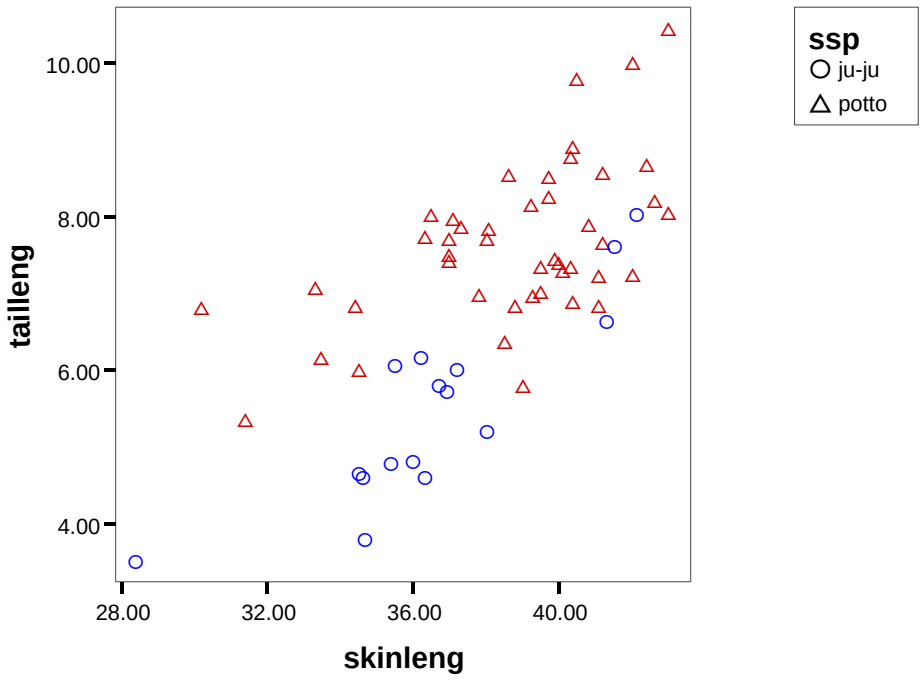


**Figure 44 Body (pelage) length versus tail length for specimens resembling descriptions of *P. p. ju-ju* and *P. p. potto***

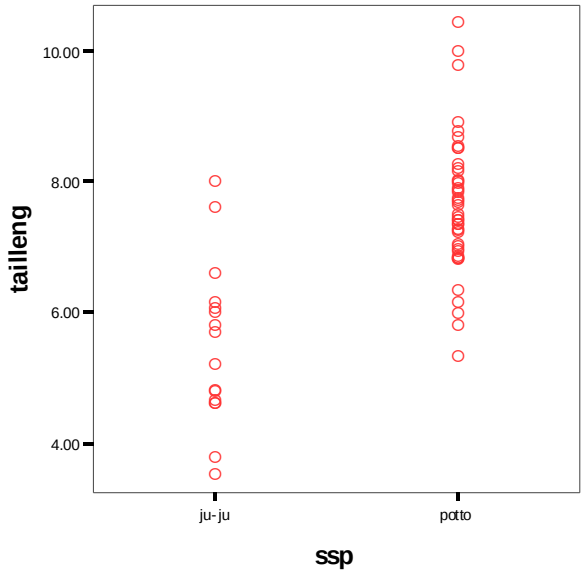


**Figure 45 Tail lengths for specimens resembling *P. p. potto* and *P. p. ju-ju***

## 6.4. Conclusion

Overall, the following post cranial diagnostic traits for potential morphs could be identified:

- Differences in tail length

# 7. PELAGE

## 7.1. Non-Metric Data

The majority of the pelages from the collections studied can be readily described as being brownish with a dark dorsal area near the shoulder region. The stripes are rarely well-defined and very often appear to be part of either a rippling pattern along the cranial-caudal dorsal midline or an elongated diffuse dark patch. The variety of the shades of brown range from light grey-brown to yellow-brown to plain brown to dark brown to red and reddish brown. Some specimens have thick white/silvery tipping to their fur—that is, the distal half or third is silvery white instead of brown. Some specimens appear to have a tripartite coloration separating their head/forelimbs, shoulders, and the posterior portion behind the shoulders. Others have a bipartite coloration separating the head from the rest of the body. Some lack such sharp color boundaries but can be separated by the relative degree of development of the dorsal stripe and overall shade differences. Furthermore, the preserved skins of some specimens are clearly larger and longer than their shorter, squatter cohorts. These observations confirm and support the reports of the range of coloration and color-patterning described in received taxonomies.

**Figure 46 Potto pelages--the top specimen demonstrates a typical *P. p. ibeanus* pattern; the rest are all labeled as *P. p. potto* despite obvious differences, especially the specimen just below *P. p. ibeanus***

The western range of *Perodicticus* is especially well represented by the collection at the USNM, and all are labeled as *P. p. potto*. The specimens from Kpodave have lighter tones, either yellowish or grey-brown. The Ghana specimens have medium brown fur with a squiggly dark brown dorsal stripe. The Ivory Coast specimens from Jacqueville have a lighter yellow tone with dark ripples focused on the cranial end of the spine. The Nigerian and Ivory Coast specimens from Guitri have blurred reddish-brown patches toward the shoulder rather than a dark squiggly

spine or patch. The Liberian specimens have darker brown tones and patchy dorsal spine with some mild reddish hues.

**Figure 47 Closeup of the distinct coloration of *P. p. ibeanus***

**Figure 48 Specimen labeled as *P. p. edwardi* demonstrating gold tipping on the fur**

**Figure 49 Posterior half of the specimen from Fig 48, *P. p. edwardsi*, showing a common pattern of color transition for members assigned to that taxon**

**Figure 50 Two patterns among the Dahomey specimens from Kpodave are presented with alternating pelages--the large type with the thin, squiggly dorsal stripe and the smaller type with the rippled appearance**

**Figure 51 A close-up of the rippled pattern of the smaller Dahomey morph, which was consistently male in this sample**

**Figure 52 A close-up of the larger Dahomey specimens, which were consistently female in this study, showing the thin, squiggly dorsal stripe**

**Figure 53 Left--pelage of specimen labeled *P. p. ibeanus*; right--specimen from Dahomey labeled *P. potto***

**Figure 54 Specimens labeled *P. potto* with similar size and pelage patterns but which are much darker and redder than those from Dahomey. The smaller specimens have a rippled appearance but in this group they are female and the larger specimens are male. The rippling may in fact be size-related not sex-related.**

**Figure 55 Close-up of a pelage of *P. potto* (a.k.a. *P. p. potto*) from Ghana showing a "burned-toast" apperance, as the wooly thick fur causes the dorsal striping to appear much more diffuse**

**Figure 56 A less strikingly defined example of a pelage with the *P. p. ibeanus* pattern (top) compared to the short, dark, squat pelage often found in specimens from Ghana from the western range assigned to *P. p. potto* (bottom)**

**Figure 57 A group of specimens of *P. p. potto* showing varying degrees of the diffuse dorsal stripe pattern**

**Figure 58 Pelages of *P. p. potto* from the Ivory Coast with extremely heavy and thickly diffused dorsal striping**

**Figure 59 The second specimens from the bottom is a light grey "*P. potto*" from Dahomey contrasted with specimens labeled "*P. p. potto*" bearing the burned toast look from the Ivory Coast and Ghana**

**Figure 60 A group of pottos assigned to *P. potto* from the Ivory Coast showing examples of diffuse and well-defined dorsal stripes**

**Figure 61 More pelages from the Ivory Coast showing a range in tone from light to dark**

**Figure 62 A close-up of the mild light tipping/strong ripple pattern, this time from a specimen from the Ivory Coast**

**Figure 63 Specimens assigned to *P. potto* (a.k.a. *P. p. potto*) from Liberia showing a very unusual pelage with an almost variegated color pattern, extremely thick fur, and light gray tones about the forelimbs**

**Figure 64 Somewhat similar to Fig 63, this Liberian specimen also has very thick fur, patchy coloration, and hints of gray about the forelimbs**

**Figure 65 Another Liberian potto, this specimen has more clearly defined coloration with the light brown zones on the head and neck separated by a dark band; the fur is still wooly and gray hairs are observed on the forelimb**

**Figure 66 This Liberian potto demonstrates a pelage pattern with straighter/darker fur toward the cranial end (left) and woolier, lighter fur toward the caudal end (right)**

**Figure 67 Liberian pottos showing the same wooly and diffuse pattern as previous figures, yet the middle specimens has a noticeably red tint, showing more variation within the Liberian theme**

**Figure 68 Below and to the right are examples of variation within a theme present in the far western range of the genus, while above/left is a specimen from Dahomey (upper middle) and a specimen of *P. p. ibeanus* (top)**

**Figure 69 Specimens labeled as *P. potto* from Nigeria--with lighter and more uniform (almost olive-like) colors--with a weak, squiggly dorsal stripe**

**Figure 70 A specimen representative of the Ivory Coast/Ghana rippled pattern (second from top) compared to the Nigerian pattern (both currently assigned to same taxon)**

**Figure 71 Specimen representing the diffuse stripe pattern from the Ivory Coast/Ghana (second from top) compared to the Nigerian potto sample**

**Figure 72 The larger specimens from Dahomey and those from Nigeria look very similar; the Dahomey specimen (center) is still more yellowish with a red tint than the flanking specimens from Nigeria. These specimens correspond to some degree with descriptions of *P. p. ju-ju*.**

**Figure 73 Specimens listed as *P. p. edwardsi* tend to have reddish hues from mild to deep brownish red. This specimen has very mild reddish hues.**

**Figure 74 Another mildly reddish specimen of *P. p. edwardsi* from the Carnegie Museum of Natural History**

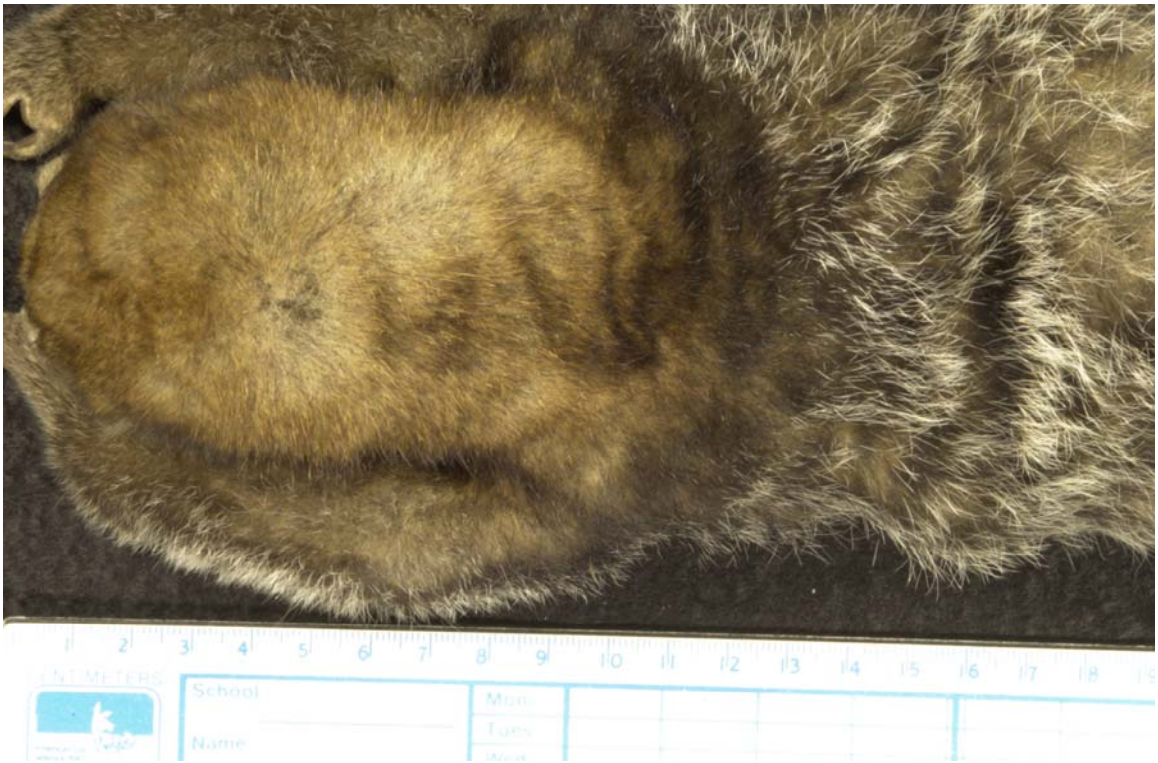

**Figure 75 Specimen of *P. p. edwardsi* demonstrating heavy silvery tipping of everywhere but the head and neck**

The specimens from the eastern range of *Perodicticus,* especially those from Kenya and Uganda, are labeled *P. p. ibeanus*. The specimens are consistently lighter brown at the head (either deeply brown or somewhat reddish), with a dark diffuse coloration around the shoulders, and a distinct darker brown or grey coloration throughout the rest of the posterior. This basic tripartite coloration is basic to *P. p. ibeanus*.

The collection at the USNM is especially well stocked with specimens from the western range of *Perodicticus*. The specimens from Kpodave and Nigeria appear to be distinct in the eastern range. They have similar coloration, although Nigeria specimens are more olive colored and

Dahomey specimens are more yellow-gray. The larger Kpodave and Nigeria specimens have a more-or-less uniform grayish color with minimal/mild/thin dark squiggly lines instead of the full dark dorsal stripes seen in specimens from more western areas. Some lack even this minimal striping. The smaller Kpodave specimens have a rippling appearance in which the lines are oriented medio-laterally and radiate along the cranial-caudal axis. This mild rippling was also observed in some other smaller specimens from the eastern zone outside of Nigeria and Dahomey.

The Ivory Coast and Ghana specimens have more mixed and heavier tones with a dark and thick patch/stripe along the cranial half of the spine. In some cases this patch is somewhat diffuse and with the brown fur background it gives the appearance of burnt toast. The Liberian specimens are among the darkest with diffuse/irregular patterning, possibly due to their highly wooly fur. The prepared skins of Ivory Coast specimens is longer than those from Ghana, and some Liberian specimens have a consistently distinct pattern of lighter fur around the head and silvery tipped fur on the forelimbs.

The central range of *Perodicticus* is strongly represented at the AMNH, with labels varying between *P. p. edwardsi*, *P. p. faustus*, and *P. p. ibeanus*. Many drawers have specimens whose labels clearly originally listed their bearers as *P. p. faustus*. These labels have a line drawn through "faustus" and above or below is written the word "ibeanus."

One noticeable pelage pattern is an excessively white-tipped coating except around the head and neck found in the Democratic Republic of the Congo (formerly Zaire) at Akenge, Avakubi, Medje, and Niangara. Another outstanding pattern is having a light to dark transition from the lateral margins moving medially (tend to be of non-reddish hues), which is found in the DPR at Medje, Niapu, and Niangara. Also very noticeable are those specimens with a striking reddish hue, not merely reddish brown but reddish, often blackened at the tips. Other colors include plainer brown and grey tones, either uniform or with off-colors/dark colors around the upper back/shoulders, found in DPR at Medje as well as Kango in Gabon.

Included among the "faustus to ibeanus" specimens are examples of all the major color patterns. Those specimens labeled as *P. p. edwardsi* included an odd assortment—one with the light-to-dark pattern; two expressing variations of a pattern with solid grey posteriorly and some degree of reddish/goldish color toward the head and neck region; another with a grey posterior and medium brown anterior; another with excessive white tipping; others with dark and deep reddish colors and some of these with long black cranial hairs and black tipping to the red fur; another with lots of long hairs, medium brown coloration, and very light around the shoulders. The redder specimens primarily come from Gabon.

Two specimens from the western range are represented at the AMNH, and both are labeled as *P. p. potto*. One specimen from Liberia (at Sawtown) appears to have the light-to-dark pattern while another from Grand Gedeh County in Liberia lacks this pattern, having a diffuse pattern of medium brownish colors and light tones with a dark dorsal stripe patch and goldish tipping on the fur.

The specimens from the eastern, central, and western range of *Perodicticus* are moderately represented at the CM. The color differences between these regions are not nearly as striking from this sample, with a couple of specimens with somewhat redder hues and one silvery tipped specimen apparent from the central region. One specimen labeled as *P. p. ibeanus* doesn't exhibit the striking tripartite color pattern of the eastern range with very sharp boundaries.

The basic pattern, medium to medium-reddish brown with a squiggly to patchy dark dorsal stripe, is very frequent in the western range and somewhat common in the central range. In the western range there is a group of lighter gray/light yellowish-brown specimens with medio-laterally oriented rippling. In the central range there are specimens with highly reddish hues. In the eastern range are the tripartite color patterns which may substitute darker grey or darker reddish hues into the posterior color. For the central and overlapping into the margin of the western range there are "tipping patterns" involving gold, silvery, and black tipped fur. Presuming that this reflects a shift from the juvenile pelage coloration to mature coloration as the hairs grow out, there are certainly different states present. In addition, there seem to be indications of color change moving cranio-caudally from the head toward the tail as well as a different pattern in which the change moves medio-laterally.

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The basic expected states from the received taxonomies, 1) medium brown with dark dorsal stripe, 2) highly reddish hues with black patches, 3) tripartite light/dark borders between the head, shoulders and trunk, 4) lighter grayish tones with mild to absent dorsal stripe, were confirmed. An alternate state, highly silvery coloration except for the head and dull grayish

tones, was also confirmed. A second alternate state, a medio-lateral darkening, has been added. In addition, the variation in the tipping has been confirmed and expanded, and the pattern of color change along the cranio-caudal axis (another potential alternate state) has been described.

It is not possible to definitively identify any of these states as "juvenile" or "mature" or "typically male" or "typically female." Both adults and subadults (from dental descriptions when the matching skull was available or the recorder's observation on the label), for example, express the excessive silvery-white tipping. This same pattern was also present whether the collection tags were dated winter, fall, or summer. While it is certainly possible that this state may persist into adulthood for a time in some specimens, it certainly calls into question the idea that there is a uniform pattern of development for the pelage in *Perodicticus*. Two infant specimens from the eastern and western range (one from USMN, one from CM respectively) expressed a yellowish pelage, though a different coloration may have developed in a later juvenile phase. The primary reference for *Perodicticus* pelage development comes from Cowgill (1969), who describes infants as going from white at birth to a grayish-white within a few days.

Potential alternate states sometimes associated with being subadult (such as the silvery coat) are present and variation exists in the expression of all character states. Since adult specimens frequently express these alternate states, if these states do in fact match the subadult state of the more typical specimens of the eastern, central, and western potto forms, then there is the potential for using heterochrony, or changes in the timing of the development and expression of traits, to explain the population differences. The fact that all of the typical forms and the

alternate forms tend to be mildly to strongly geographically distinct makes the resolution of these questions even more complicated.

## 7.2. Metric Data

Hair lengths were not measured as a part of this study.

## 7.3. Summary

Although there were some weak correlations between size and pelage patterns, there was nothing metric or non-metric that divided males and females.

There are at least four main character states for the pelages of the genus *Perodicticus*—

- light brown head/forelimbs, dark shoulders, uniform grey to reddish brown posterior
- highly reddish hairs mixed with diffuse black around the shoulders and very long hairs around the head
- light yellow-gray to olive gray with a mild to absent thin/squiggly dorsal stripe
- medium to dark brown with either a distinct dorsal stripe/set of stripes or diffuse dark dorsal patch

The alternate state to the latter two pelages, often found in slightly smaller individuals, is a wavy pattern along flowing along the cranio-caudal axis. In addition, the latero-medial light to dark pattern and the heavy silvery-tipped pattern are found in the same regions as the first two regular

character states. In Liberia there was distinct pattern of lighter fur around the head and grey tipped fur on the forelimbs. The degree to which these alternate morphs are associated with sex, age, heterochrony, or simply absolute size differences is unclear and is in need of further investigation.

With regard to the descriptions of the traditional taxonomy, the "light brown head/forelimbs, dark shoulders, and uniform grey to reddish brown posterior" profile matches the configuration described for *P. p. ibeanus*, the expected range for that taxon, and generally the specimens which have been labeled thus. The "highly reddish hairs mixed with diffuse black around the shoulders and very long hairs around the head" profile tends to correlate to specimens from the central portion of the range of *Perodicticus* with large molar teeth, which would be expected for both specimens of *P. p. edwardsi* and *P. p. faustus*. The "light yellow-gray to olive gray with a mild to absent thin/squiggly dorsal stripe" profile may in fact indicate validity to the taxon *P. p. ju-ju* as it does occupy the proper area and loosely matches the pelage description given for that taxon. However, the tails of these specimens are not as long as other specimens labeled *P. p. potto* in the western range of the genus, and this was a descriptive feature in the traditional literature identifying that taxon. The localities and a pelage profile of "medium to dark brown with either a distinct dorsal stripe/set of stripes or diffuse dark dorsal patch" conform to the expectations for *P. p. potto*.

## 7.4. Conclusion

Overall, the following pelage-based diagnostic traits for potential morphs could be identified:

- light brown head/forelimbs, dark shoulders, uniform grey to reddish brown posterior
- highly reddish hairs mixed with diffuse black around the shoulders and very long hairs around the head
- light yellow-gray to olive gray with a mild to absent thin/squiggly dorsal stripe
- medium to dark brown with either a distinct dorsal stripe/set of stripes or diffuse dark dorsal patch
- a wavy pattern along flowing along the cranio-caudal axis.
- a latero-medial light to dark pattern and the heavy silvery-tipped pattern
- a distinct pattern of lighter fur around the head and grey tipped fur on the forelimbs

# 8. TESTING TAXONOMIES

The review and comparison of metric and non-metric descriptions from previous potto taxonomies to those collected in this study do confirm that regional differences within the taxon *Perodicticus* do exist and are distributed in more or less stable patterns. The correlations between the previous descriptions and the current study results are discussed by taxon.

## 8.1. Individual Taxa

### 8.1.1. *P. p. edwardsi*

#### 8.1.1.1. Distinguishing Features in the Literature for This Taxon

Whereas having very large cheek teeth relative to other specimens of *Perodicticus* is descriptive of *P. p. edwardsi*, it is also descriptive of *P. p. faustus*. In fact, *P. p. faustus* is considered a synonym for *P. p. edwardsi* in contemporary literature. However, *P. p. edwardsi* is also described as having the largest values for maximum cranial length, whereas *P. p. faustus* is listed as ranking with *P. p. potto* in having the smallest average values for this measurement.

#### 8.1.1.2. Study Results

Those specimens labeled as *P. p. edwardsi* clearly had the largest teeth in both the length and width of the first two upper and lower molars. The specimens labeled as *P. p. ibeanus* and *P. p. potto*, including potential representatives of *P. p. faustus* and *P. p. ju-ju*, had much smaller teeth.

The specimens from Cameroon by far had the largest teeth, with Equatorial Guinea (French Equatorial Africa) and Gabon having the next largest molar sizes. These regions all occur in the central part of the potto range, the area predominantly associated with *P. p. edwardsi*. Congo and the Central African Republic are also in the central zone and also had large values for the molars, especially the width of $M^2$.

The values for maximum cranial length were supposed to be largest for *P. p. edwardsi* and those specimens with the large molars from the designated localities of that taxon did indeed fulfill that expectation.

The "highly reddish hairs mixed with diffuse black around the shoulders and very long hairs around the head" pelage profile tends to correlate to specimens from the central portion of the range of *Perodicticus* with large molar teeth, which would be expected for both specimens of *P. p. edwardsi* and *P. p. faustus*.

#### 8.1.1.3. Discussion

A fascinating taxon to assess was *P. p. edwardsi* (formerly *P. edwardsi*, syn. *P. batsei*), which occupies the central part of the potto range, including Equatorial Guinea, Cameroon, Gabon, and the Central African Republic. Many specimens did possess strikingly deep red pelage with heavy black tips and extremely long guard hairs about the head and face, while others were milder red, or had an odd medio-lateral shift from light to dark fur. Still others were long and bland grey unlike any other described taxon for the genus. Within these groupings were large amounts of variation. The revealing feature was the size of the cheek teeth, especially the width of the molars, which were the largest of any pottos studied. The noted reddish fur and large cheek teeth correspond to taxonomic descriptions from Oldfield Thomas (1910a), Ernst Schwarz (1931a), Osmand Hill (1953), and Jenkins (1987). While there is a general correspondence between the results of this study and previous descriptions, it is the opinion of this researcher that all studies (including this one) point to the likely possibility of either multiple taxa being subsumed within *P. p. edwardsi* or some phenomenon producing large amounts of diversity in that region or both. This taxon is distinct from other pottos but it may actually comprise several additional taxa, so it is provisionally reliable.

### 8.1.2. *P. p. faustus*

#### 8.1.2.1. Distinguishing Features in the Literature for This Taxon

As mentioned under the description of *P. p. edwardsi*, both *P. p. edwardsi* and *P. p. faustus* share the description of having the largest cheek teeth among pottos, but *P. p. edwardsi* is listed as having the largest values from maximum cranial length and *P. p. faustus* is listed as having among the smallest values for that measurement. Both taxa also share the description of having very reddish fur.

#### 8.1.2.2. Study Results

The results for the dental diagnostic traits are the same as those for *P. p. edwardsi*. The central portion of the range of *Perodicticus*, the range for both *P. p. edwardsi* and *P. p. faustus*, did indeed have a population with the largest molars, especially by width. The only truly distinguishing trait listed for *P. p. edwardsi* and *P. p. faustus* was skull size. Only one of the large-toothed pottos of the sample from the central range of the genus, AMNH 54340 from the Swanke region of the Congo, had a recorded maximum cranial length of 6.09 cm, a maximum cranial length size in the expected range for *P. p. faustus.*

As stated in the results for *P. p. edwardsi*, the "highly reddish hairs mixed with diffuse black around the shoulders and very long hairs around the head" profile tends to correlate to specimens

from the central portion of the range of *Perodicticus* with large molar teeth, which would be expected for both specimens of *P. p. edwardsi* and *P. p. faustus*.

#### 8.1.2.3. Discussion

The most difficult group to assess was *P. p. faustus*. It's description is very much like that of *P. p. edwardsi*, and that is certainly one of the more compelling reasons to make the taxon *P. p. faustus* a synonym of *P. p. edwardsi*. One specimen did have the larger molars and the smaller skull size predicted by the descriptions of the traditional taxonomies, but whether this was a genuine representative of a separate taxon apart from *P. p. edwardsi* or just a smaller-skulled example of *P. p. edwardsi* is impossible to say. The validity of this taxon is questionable.

### 8.1.3. *P. p. ibeanus*

#### 8.1.3.1. Distinguishing Features in the Literature for This Taxon

Dentally, *P. p. ibeanus* has been described as being distinct in having the second upper molar smaller than the first. Post-cranially it is supposed to have a relatively long tail. However, the primary distinguishing feature listed for this taxon is the pelage, which has a head of one color, a field of darkened to black fur across the shoulders, and then a third color for the rest of the trunk and tail.

#### 8.1.3.2. Study Results

The specimens labeled as *P. p. ibeanus* as well as specimens identified only as being from Kenya and Uganda, the range of *P. p. ibeanus*, have $M^2$ length shorter than $M^1$ length but $M^1$ is wider than $M^2$, which corresponds somewhat to the expectation from the literature. The observation that *P. p. ibeanus* has a "relatively" longer tail seems false if the basis for comparison is other pottos. The "light brown head/forelimbs, dark shoulders, uniform grey to reddish brown posterior" pelage profile matches the configuration described for *P. p. ibeanus* and specimens having this profile matched the expected portion of the geographic range for that taxon.

#### 8.1.3.3. Discussion

The most readily spotted taxon is *P. p. ibeanus* (formerly *P. ibeanus,* syn. *P. faustus*), which is described as occupying the eastern-most part of the potto range, including Kenya, Uganda, and the Democratic Republic of the Congo (formerly Zaire). Their large pelages, with the distinctive tripartite coloration, corresponds well to the monograph by Oldfield Thomas (1910b) as well as descriptions from Ernst Schwarz (1931a) and Osmand Hill (1953). The tail is not typically as long, however, as might be expected from the taxon's original description. The measurements in this study generally accord with those offered by Schwarz (1931a) and Jenkins (1987). No novel features were discovered which might further distinguish any or all members of this group. The taxon is reliable, but the morph is distinguished primarily by overall body size and coloration.

### 8.1.4. *P. p. ju-ju*

#### 8.1.4.1. Distinguishing Features in the Literature for This Taxon

While the teeth of *P. p. ju-ju* are described as being similar to the teeth of *P. p. potto*, the skull of *P. p. ju-ju* is supposed to be considerably larger than that of *P. p. potto*. In addition, *P. p. ju-ju* is described as having a proportionally long tail. This is interpreted here as meaning relatively long for a potto of a particular body size. The pelage is also supposed to be distinctive, a drab grey with no appreciable dark patch on the upper back.

#### 8.1.4.2. Study Results

The "light yellow-gray to olive gray with a mild to absent thin/squiggly dorsal stripe" profile may in fact indicate a validity to the taxon *P. p. ju-ju* as it does occupy the proper area and loosely matches the pelage description given for that taxon. However, the tails of these specimens are not as long as other specimens labeled *P. p. potto* in the western range of the genus, and this was a descriptive feature in the traditional literature identifying that taxon. In addition, there was no appreciable difference is skull size between the specimens tentatively identified as *P. p. ju-ju* and those identified as *P. p. potto*.

#### 8.1.4.3. Discussion

The issue of the viability of ju-ju, either as it is currently known, *P. p. ju-ju*, or by its former rank, *P. ju-ju*, has been called "the main controversy" in potto taxonomy (Jenkins 1987). Although Jenkins cites researchers who support the viability of the taxon (i.e. Hill 1953, Grubb 1980), she ultimately agrees with Schwarz (1931a) that it should be sunk and combined with another taxon. She argues that since *P. p. ju-ju* specimens can (for the most part) be comfortably assigned to either *P. p. potto* or *P. p. edwardsi*. Specimens from Dahomey (now Benin) and to a lesser extent specimens from Nigeria at the USNM do not conform to this view. The overall size, the pelage coloration, and the degree to which the tails and molar teeth are notably smaller than either *P. p. potto* or *P. p. edwardsi* (respectively) suggest that *P. p. ju-ju* does not readily fit in other taxa and should be retained as a separate group. The specimens referred to hear as *P. ju-ju*, from Dahomey and Nigeria, tend to share the expanded mesial keel shaped like a bowed fin on the lower anterior premolar. The question of whether this indicates a shared ecological problem with the members of *P. p. potto* (who also possess this trait), a common ancestor with *P. p. potto* to the exclusion of other pottos, or high levels of gene flow between *P. p. ju-ju* and *P. p. potto* remains unresolved. However, part of the debate may also be confusion over the characterization of *P. p. ju-ju*, which may be confused with odd members of *P. p. potto* which were observed in this study (for example, see the figures displaying photographic evidence of 'oddballs' from Liberia, Figures 63-65). There are certainly traits available to distinguish a geographic subset of *Perodicticus*, and given some similarity to a previously named taxon, that name, *P. p. ju-ju*, has been adopted here. However, the long tail and large skull of *P. p. ju-ju*

were not present in these specimens, and it can also be argued this morph should be given a different name. But whatever it is called, the taxon would be valid.

### 8.1.5. *P. p. potto*

#### 8.1.5.1. Distinguishing Features in the Literature for This Taxon

Dentally, the descriptions distinguish *P. p. potto* by suggesting that $P^2$ is a little larger than $P^3$ while $P_2$ is a little smaller than $P_3$. In similar description, the "foremost" of the lower premolars is supposed to be smaller than those teeth that follow it. Given that the caniniform tooth situated disto-laterally from the toothcomb is considered to be a premolar, designated $P_2$, in this study it is presumed that the $P_2$ or foremost premolar is what is described in the data sections as $P_3$ or the middle lower premolar. Also, *P. p. potto* is supposed to have the smallest molar teeth, even smaller than *P. p. ju-ju*.

#### 8.1.5.2. Study Results

The localities and a pelage profile of "medium to dark brown with either a distinct dorsal stripe/set of stripes or diffuse dark dorsal patch" conform to the expectations for *P. p. potto*. The western range of the genus is associated with *P. p. potto*. Specimens from the western range of *Perodicticus*, especially those from Ghana and the Ivory Coast, do frequently have a small middle (lower and sometimes upper) premolar. Specimens from Ivory Coast and Ghana also happened to have some of the smallest overall molar sizes.

Also predominantly in the western part of the pottos' range is a new feature—a bowed mesial edge shaped to varying degrees like a fin on the lower anterior (caniniform) premolar.

#### 8.1.5.3. Discussion

The taxon known as *P. p. potto* (formerly *P. potto*) occupies the westernmost part of the potto range, including Sierra Leone, Ivory Coast, Ghana, and Liberia. Specimens from this area tended to fit previous descriptions, especially Osmand Hill (1953). In fact, specimens from that region most commonly displayed the broad dorsal stripe associated with the genus. However, they share a previously unrecognized feature on its lower anterior premolar (a swollen mesial keel) and have the longest tail of any potto (in both relative and absolute terms) despite being one of the smallest pottos. Measurements taken for this study tend to conform to those from traditional taxonomies. The taxon appears to be reliable.

## 8.2. Distribution Patterns of Assessed Traditional Taxa

The patterns of dental and pelage differences are represented for the entire range of the taxon.

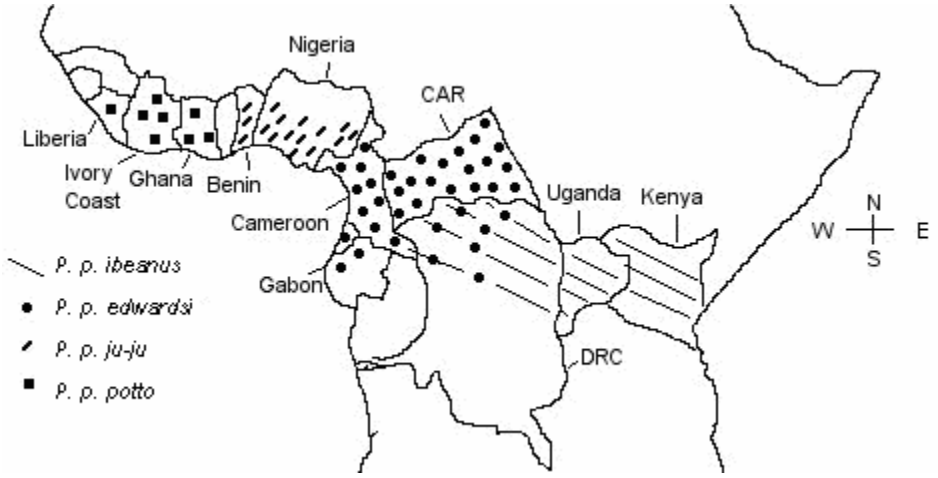


**Figure 76 The distribution of specimens with pelage patterns corresponding to traditional taxonomies, including possible specimens of *P. p. ju-ju* as assessed in this study.**

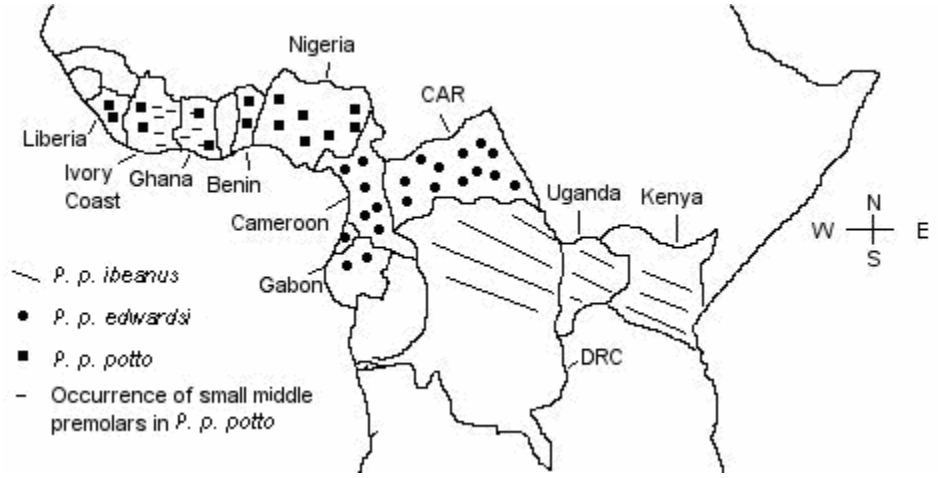


**Figure 77 The distribution of specimens with dental features corresponding to traditional taxonomies, such as the large molars of *P. p. edwardsi*. *P. p. potto* in the legend corresponds to the range of the newly described bowed-fin on lower anterior premolars**

Many of the differences described in this study were distributed in clinal, semi-clinal, and regionally distinct patterns. The overlap of these variations produces unique configurations which form the basis of naming recognizable groups in nature. Two of the more controversial taxa, *Pseudopotto martini* and *P. p. ju-ju*, are highlighted in this study.

The results provide a clearer context for the interpretation of *Pseudopotto martini*. Examples of a reduced upper anterior premolar were primarily concentrated to a small part of the western range of *Perodicticus* while partially and fully formed entepicondylar foramina were found throughout the known range of the pottos. Major regional differences in tail length were also observed in *Perodicticus*. Other features listed as distinctive to *Pseudopotto* were not observed in the sample. Whether or not the taxon is accepted or rejected, the results of this study add to the context of the type and degree of variation expected for pottos and closely related forms.

The proper form of taxonomic recognition for *P. p. ju-ju* (formerly *P. ju-ju*) is contested (Grubb 1978, Jenkins 1987). While it has been suggested that it represents an intermediate form, it appears to be the product of overlapping *and* unique patterns of variation. The dentition more closely resembles *P. p. potto*, thought he molars are notably smaller. The tail is more similar to *P. p. edwardsi*, and again tends to be much smaller in the east and longer toward the west approaching the range of *P. p. potto*. The pelage color better matches specimens of *P. p. potto* further to the west, yet the pelage pattern tends to remain distinct.

Explanations for the manner in which differences are distributed within and between taxa rely on mechanisms such as sexual selection, natural selection, or genetic drift and may or may not be linked to speciation events depending on the model of diversification embraced. These results support the notion that multiple, often overlapping mechanisms operating in a population is more likely the rule rather than the exception.

The differences in tooth size and morphology, pelage/body size morphs, and post-cranial variations within this taxon have been ranked as significant at the generic, specific, subspecific, or no official taxonomic level. These designations are based on methodological and theoretical preferences, the types of questions required by the taxonomy in use, and the expertise of the taxonomist conducting the survey. Such differences are common in the received taxonomies of primates.

Regardless of taxonomic rank there is a great deal of variability to be preserved and explored in *Perodicticus*. These population differences in nocturnal mammals are relevant to concerns about viewing traits as biological outcomes versus taxonomic indicators and the potential for cryptic speciation. Documentation of all common differences despite prevailing taxonomic attitudes toward lumping or splitting are essential for generating and testing models of evolutionary processes.

## 8.3. Taxon-Free Summary of Potential Diagnostic Traits for Recognizing Morphs in the genus *Perodicticus*

Overall, the following dental diagnostic traits for potential morphs could be identified:

- The presence or absence of a stepwise pattern of the upper canine-premolar series versus a non-stepwise pattern, identified by Schwartz and Beutel (1995)

- The presence or absence of a tiny middle lower and upper middle premolar

- The presence or absence of relatively large cheek teeth, especially the width of the molars

- The presence or absence of a bowed fin on the mesial keel of the lower anterior caniniform premolars

- The stepwise pattern (or lack thereof), the diminutive middle anterior (upper or lower) premolar, and the bowed fin on the lower anterior premolars are not mutually exclusive traits.

Overall, the following cranial diagnostic traits for potential morphs could be identified:

- Differences in maximum cranial length
- Differences in maximum cranial width

Overall, the following post cranial diagnostic traits for potential morphs could be identified:

- Differences in tail length

Overall, the following pelage-based diagnostic traits for potential morphs could be identified:

- light brown head/forelimbs, dark shoulders, uniform grey to reddish brown posterior

- highly reddish hairs mixed with diffuse black around the shoulders and very long hairs around the head
- light yellow-gray to olive gray with a mild to absent thin/squiggly dorsal stripe
- medium to dark brown with either a distinct dorsal stripe/set of stripes or diffuse dark dorsal patch
- a wavy pattern along flowing along the cranio-caudal axis.
- a latero-medial light to dark pattern and the heavy silvery-tipped pattern
- a distinct pattern of lighter fur around the head and grey tipped fur on the forelimbs

# 9. DISCUSSION

## 9.1. Review of Hypotheses

The general hypotheses used for this study were:

**"The taxa previously recognized as species and later demoted to subspecies within the group *Perodicticus* constitute robust morphs, that is, they are phenotypically well-distinguished from other specimens attributed to the genus *Perodicticus*."**

**"There are no morphs which can be identified within the specimens attributed to *Perodicticus* which would lump or split the currently recognized subspecies."**

- The hypotheses suggest the following predictions:

- There will be no unrecognized/mischaracterized novelties in the dentition

- There will be no unrecognized/mischaracterized novelties in the cranium

- There will be no unrecognized/mischaracterized novelties in the post-cranium

- There will be no unrecognized/mischaracterized novelties in the pelage

One reason for selecting the hypotheses was to assess whether unrecognized or unappreciated differences exist within the museum specimens assigned to the genus *Perodicticus*. Another value of testing these hypotheses is that evolutionary studies rely on sufficiently accurate taxonomies.

Hence, in addition to supplementing the taxonomic literature with verification and documentation of novel and previously suggested traits for this genus, many more hypotheses are generated by the results. Specimens were examined from collections at the beginning up to the middle of the twentieth century and were reasonably distributed across seasonal periods. This does not discount seasonal explanations but it does diminish their likelihood for many of the more robust patterns. The potential differential effect of long-term preservation on coloration (based on differences in age and method) is also another intriguing question raised by this study to account for distinctions in pelage observed. Because of the cryptic nature of this nocturnal

group, there is also an open question as to whether small-scale influences of local predator-prey relationships accounts for the any perceived pelage differences or whether larger scale factors such as equatorial climate changes or other stressors may have a greater impact on the phenotype.

If there are no regularly occurring differences other than general body/tooth size and mild pelage variation, then *Perodicticus* is a suitable model for examining how and why a population distributed over such a wide area has not undergone more significant regional differentiation. If there are regularly occurring differences other than general body/tooth size and mild pelage variation, then *Perodicticus* is a suitable model for examining how and why such a population has become regionally differentiated. In the latter case taxonomic nomenclature may also be challenged. In either case, further study on intra-taxic genetic differences as well as regional ecological differences are in order.

## 9.2. Review of Results

An extensive summary of the results is presented in Chapter 8. A concise review is offered here.

Examining the dentition confirmed that different groups of pottos do vary by tooth size. Specimens from countries in the central zone of the pottos' range tended to have the largest teeth, especially those from Cameroon, Equatorial Guinea, and Gabon. The teeth from the eastern and western zones were comparably smaller. Specimens from Ghana, Ivory Coast,

Dahomey (western range) and Kenya (eastern range), and the DRC (central range), in particular, tended to have notably small values for the length and width of their molars.

Specimens from the western range of *Perodicticus*, especially those from Ghana and the Ivory Coast, do frequently have a small middle (lower and sometimes upper) premolar. Specimens from Ivory Coast and Ghana also happened to have some of the smallest overall molar sizes. Also predominantly in the western part of the pottos' range is a new feature—a bowed mesial edge shaped to varying degrees like a fin on the lower anterior (caniniform) premolar. The stepwise pattern of the upper canine-premolar series versus the non-stepwise pattern identified by Schwartz and Beutel (1995) was confirmed throughout the range of *Perodicticus*.

There were distinct differences in tail length both relative to other appendages as well as in absolute length. Specimens labeled *P. p. ibeanus* from Kenya have relatively short tails. Specimens of *P. potto* (often assigned as *P. p. potto*) from Dahomey have primarily short tails. Specimens of *P. potto potto* from Nigeria are split between short and medium tails. Specimens of *P. p. potto* from Ghana, Ivory Coast, and Liberia have predominantly long tails.

There are at least four main character states for the pelages of the genus *Perodicticus*—

- light brown head/forelimbs, dark shoulders, uniform grey to reddish brown posterior
- highly reddish hairs mixed with diffuse black around the shoulders and very long hairs around the head
- light yellow-gray to olive gray with a mild to absent thin/squiggly dorsal stripe

- medium to dark brown with either a distinct dorsal stripe/set of stripes or diffuse dark dorsal patch

The alternate state to the latter two pelages, often found in slightly smaller individuals, is a wavy pattern flowing along the cranio-caudal axis. In addition, the latero-medial light to dark pattern and the heavy silvery-tipped pattern are found in the same regions as the first two regular character states. In Liberia there was distinct pattern of lighter fur around the head and silvery tipped fur on the forelimbs. The degree to which this is associated with sex, age, heterochrony, or simply absolute size differences is unclear and is in need of further investigation.

The correspondence of dental, cranial, and pelage traits previously associated with the taxa *P. p. ibeanus*, *P. p. edwardsi*, and *P. p. potto* are for the most part a good fit. It is presumed for this study that the clear differences present in the Dahomey and Nigeria specimens should be assigned to the subspecies *P. p. ju-ju*, primarily based on the reported location of previously assigned specimens of this taxon. Should this not be the case then a new taxon is most certainly warranted to outline and highlight this distinctive group of specimens. It is still unclear whether specimens previously attributed to *P. p. faustus* (especially those studied at the AMNH) should be kept in *P. p. ibeanus*, moved to *P. p. edwardsi*, or resurrected as a separate taxon. Only one specimen matched the expectations of cranial and molar size for *P. p. faustus*.

In addition to verifying and supporting suggested or disputed taxa by confirming previous descriptive and metric data, novel features have also been identified such as the bowed fin on the lower anterior premolar and the extreme difference in tail lengths. Many of these features were

best represented by country of origin, presenting a pattern which shows morphoclines in pelage colors, dental measurements, non-metric dental differences, and tail lengths:

- The western zone specimens tend to have long tails, a bowed fin on the lower anterior premolar, medium to dark brown fur with thick dark dorsal stripes or patches, smaller molars, and in some locales highly reduced middle premolars

- The region on the border of the western and central zones had specimens that still tend to have smaller teeth but the pelage is lighter and more uniform tending toward yellow or olive grey, the dorsal stripe is thin or absent, and tails are noticeably shorter

- The central zone specimens have darker brown tones as well as many areas with extremely reddish pelages, the molar teeth are the largest of all the pottos.

- The eastern zone specimens have smaller molars and shorter tails along with a distinctive tripartite coloration separating the head and forelimbs, the darker shoulders, and the remaining posterior portion of the body

## 9.3. Implications for Taxonomy and Systematics

As discussed in Chapter 8, the previous descriptions of regional differences associated with the naming and identification of established taxa were mostly confirmed. In other words, someone

wishing to validate the basic observations used to establish the previously named groups can find sufficient samples matching received taxonomies. The relative consistency and reliability of the established taxa compared to the relevant literature are addressed on a taxon by taxon basis in Chapter 8, with the result that there is no pressing argument to abolish these taxa. They may be lumped or split into other taxa as theory and evidence warrants, but they are retained here for convenience.

In addition to the data collected in this study, other data has a bearing on the taxonomic and systematic considerations of *Perodicticus*. The study of dental eruption by Schwartz (1974) points to a major developmental difference between those specimens labeled *P. p. faustus* and *P. p. edwardsi* and those specimens labeled *P. p. ibeanus*. *P. p. ibeanus* differs from the former group in "1) a generally earlier appearance of the permanent dentition, 2) the appearance of the upper incisors prior to, rather than at the same time as, the toothcomb, 3) the appearance of $P_4$ and then $P_3$ prior to, rather than after, $P^4$ and then $P^3$, respectively, 4) the appearance of the upper canine prior to, rather than after, $P^2$, and 5) the appearance of $M^3$ prior to, rather than after, $P^4$," (Schwartz 1974:98). The magnitude of these differences is compared to species-level differences in *Tarsius*, *Propithecus*, and *Lemur*.

On the molecular side, Christian Roos (personal communication, 2004) cites a within-group comparison based on a small sample of the three primary subspecies ("ibeanus", "edwardsi", and "potto") looking at differences in the mitochondrial cytochrome b gene sequence. The differences between the three potto taxa studied were between 7 and 9%, which is comparable to

species-level differences in the same gene for *Nycticebus* taxa (3 to 13% difference) and *Microcebus* (4 to 14% difference).

If one uses reproductive criterion as the sole (or primary) consideration for defining species, then the picture is unclear, since all pottos can procreate together but it is unclear which groups regularly do or do not do so in the wild. If the establishment of significant differences in phenotype, often referred to as diversity, is the primary criterion for defining species, then the morphology, development, and genetics definitely point to species-level differences existing in the genus *Perodicticus*. The four useful subspecies designations (the three primary labels plus "ju-ju") are useful for identifying significant regional differences whatever their origination or the proper *taxonomic rank for such combinations of differences. If only P. p. potto or P. p. ju-ju* along with *P. p. ibeanus* were known, it is almost certain that the western and eastern groups would be placed in separate "well-marked" species if not separate genera.

As for systematic comparisons, the members of *Perodicticus* can be distinguished dentally by: low rounded cusps on their molars; having both $I^1$ and $I^2$ thicker and flatter than those of *Loris* or *Arctocebus* and more like the $I^1$ of *Nycticebus*; a propensity for developing really small $M^3$s, sometimes as small as one-quarter or one-fifth the size of the other two upper molars. *Perodicticus* has been distinguished post-cranially by having the longest tails of any of the lorisids, though the longest potto tail is far shorter than the smallest tail of a member of the taxon Galago.

Within *Perodicticus*, *P. p. ju-ju* can be linked with *P. p. potto* based on the abundant presence of the bowed fin premolar in both groups, while those specimens labeled *P. p. faustus* and *P. p. edwardsi* (now mostly lumped together under "*edwardsi*") can be placed together based on tooth size and dental development. *P. p. ibeanus*, both in size and pelage, stands out from both the *P. p. potto* group and the *P. p. edwardsi* group. There is no outstanding synapomorphy that links *P. p. potto/ju-ju* to *P. p. edwardsi/faustus*, *P. p. potto/ju-ju* to *P. p. ibeanus*, or *P. p. edwardsi/faustus* to *P. p. ibeanus*. It is true that *P. p. edwardsi* and *P. p. ibeanus* tend to lack the bowed fin premolar, but notwithstanding the occasional *Nycticebus* specimen showing signs of this trait it appears to be a primitive condition for lorisids and for prosimians in general.

## 9.4. Significance of Study

The results of the study demonstrate that while the general picture provided by traditional taxonomies was fairly accurate, it was not complete either. Given the sample size of this study, it would not have been unreasonable to speculate that previously unrecognized morphological features of potential taxonomic importance would have been overlooked. Yet such features were documented. The importance of these results can be viewed in terms of the biological questions on which they may have a bearing.

The taxonomic situation of the genus *Perodicticus* offers insight into the task of trying to organize nature. This study set out to confirm and discover one particular (and particularly important) outcome of various biological and evolutionary processes, namely morphological differences. Based on previous research, the current study, and desirable future research, the implications of this study can be anticipated to some degree.

### 9.4.1. Viewing the Results as Intraspecific Variation

If the current taxonomy is retained, the study clearly calls for *P. p. ju-ju* to be maintained as one of at least four subspecies, the other three being *P. p. potto*, *P. p. edwardsi*, and *P. p. ibeanus*. This study projects and strengthens the view of genus *Perodicticus* as a group with great potential for studying how regional variations arise and are maintained across a relative large area. This would include genetic, developmental, and ecological factors contributing to the stable recreation across generations of the same distinguishing characteristics that separate the subspecies.

### 9.4.2. Viewing the Results as Interspecific Variation

If the current taxonomy is revised, the results of this study and previous studies suggest that the three primary species to be recognized, based solely on morphology, are *Perodicticus potto* from the western zone, *Perodicticus edwardsi* from the central zone, and *Perodicticus ibeanus* from the eastern zone. *P. p. ju-ju* is also morphologically distinct in many of the same features that distinguish the other three groups and an argument could be made to also elevate it to species

status as well. If it is retained as a subspecies it would be difficult to assign either to *P. potto* or *P. edwardsi*, though the shared bowed fin on the lower anterior premolar could be used to justify placing *ju-ju* as a subspecies of *P. potto*.

Under the Biological Species Concept, the change in the taxonomic status of these taxa would require genetic data or field observations displaying some form of reproductive isolation, and currently such verification of isolation is lacking. Still, they do fit the profile for the geographic isolation model of speciation. The range of the pottos is frequently divided by rivers and mountains. On the other hand, under the Recognition Species Concept, more subtle clues to mate choice would need to be uncovered. It has been documented that pottos possess glands under the skin in the urogential area which secret a pungent substance (Montagna 1962) which may be applied to offspring in a sex-specific fashion (Epps 1974, Manley 1974). It has not been confirmed whether this substance does or does not vary by region or morphology or that it has any impact on mate choice among the pottos. It is also true that pottos possess extremely elongated spinous processes on the vertebrae of their nuchal region, and that the overlying skin is highly invested with nerves relaying tactile sensations (Montagna 1962), and that they seem to be important to interpersonal relationships (Walker 1970). It is possible that the preferred manner of stimulating this area or relative degrees of sensitivity may affect socialization and therefore is a candidate for a mechanism of mate choice.

For the Phylogenetic Species Concept, an argument could be made that the difference in tail length sets some western pottos apart from the rest. A similar argument could be made for the potential autapomorphy of the bowed fin on the lower anterior premolar of some primates.

However, these two traits create incompatible groupings, so an argument would need to be advanced why one feature should be privileged over another. Also, the differences in pelage could be used to assign species rank, though the occasional oddball would present problems in some cases for establishing clear boundaries by pelage pattern and coloration.

As is the case if these differences are merely accorded the title intraspecific variation, the underlying causes for the stable replication of these differences across generations would still be an important area of study.

### 9.4.3. Context for Conservation

Regardless of whether these potto groups are assigned specific or subspecific rank, they represent different versions of the same theme. However they came to have their current differences or to occupy their current habitats, the differences are valid and important to they study of primate evolution. Should the habitat of *P. p. potto*, *P. p. ju-ju*, *P. p. edwardsi*, or *P. p. ibeanus* become threatened or their population dwindle, they should be protected as significant ecological units as per the regulations and documentation of the appropriate regulatory agencies.

### 9.4.4. Context for Taxonomic Revisions in Related Groups

The literature on galago taxonomy was previously described as displaying a pattern of recognizing increased diversity (i.e. splitting one taxon into several or elevating subspecies to the species level). The ease with which the loud night calls of the galagos potentially fit a model of

mate recognition appears to account for a good deal of this taxonomic revision. Unlike the loud, frenetic, leaping galagos, pottos are mostly quiet and slow moving (Oates 1984). This does not mean that they do not potentially possess features which are relevant to a specific mate recognition system, but it does mean that such signals, if they are present, are less obvious to human observers.

### 9.4.5. Context for *Psuedopotto*

The description of *Pseudopotto martini* includes among its distinguishing characteristics (i.e. those things which set it apart from *Perodicticus*) a very elongated tail, the presence of an entepicondylar foramina on the distal ends of the humeri, and very small oddly shaped upper middle premolar (Schwartz 1996). This is not an exhaustive list of the features described which set apart *Pseudopotto*. However, it should be noted that (relatively) long tails were found in the western range of pottos, though not as long as tails of specimens attributed to *Pseudopotto*, and entepicondylar foramina were discovered across the entire potto range. These traits were not found exclusively with other distinguishing *Pseudopotto* traits. In addition, the tiny middle premolar in some western zone pottos, while not as oddly shaped as described for the type specimen of *Pseudopotto*, is similar enough to warrant mention. Although the type specimen was not examined in this study, a photograph of the juvenile specimen suggests it may have the bowed fin on the lower anterior premolar typically present in the western range and occasionally occurring along the western border of the central zone.

These observations suggest that the list of distinguishing features for *Pseudopotto martini* may need to be revised since some of them clearly are present in the general *Perodicticus* population. However, without having examined the type specimen or other materials subsequently assigned to this taxon, it is not helpful to speculate based on the validity of the taxon based solely on the results of this study. Should the taxon *Pseudopotto martini* receive further validation, the results of this study will be helpful in providing it a more accurate systematic context.

### 9.4.6. Generation of Hypotheses and Research Questions

The results of the study generate further hypotheses and questions to be addressed. For example:

- Do the different pelage patterns reflect developmental variations by age, size, sex, heterochrony, and/or arrested development?

- Do these pelage patterns indicate interesting patterns of intraspecific variation or cryptic species?

- Will new genetic methods for identifying reproductive isolation reveal interesting patterns within or between the subtaxa of the genus?

- What are the genetic and ecological components of the bowed fin on the lower anterior premolars of some pottos? Of differences in molar size?

- Do the many distinctions of the Dahomey (and to a lesser extent Nigeria) specimens indicate a hybrid zone or a separate taxa?

  - How many taxa are actually subsumed under the name *P. p. edwardsi*?

- How do the differences in tail length affect systematic hypotheses using this feature as a simple ranked character for the genus *Perodicticus*?

- What other morphologies, especially in the post-cranial skeleton, may further distinguish or identify subtaxa in the genus?

## 9.5. Areas for Future Research

### 9.5.1. Genetics

One question which immediately comes to mind when viewing the results of a morphologically based assessment of received taxonomies is what the genetic components look like. What kinds of chromosomal, nuclear DNA, or mitochondrial DNA differences are present in the population and do these differences support the groupings suggested by the morphological analysis? While genetic samples have been taken from pottos for use in larger studies in taxonomy and systematics, published work examining differences between proposed subspecies within the

genus *Perodicticus* are rare. De Stefano and Fermenti (1974) published such a study examining the differential DNA content in lymphocytes.

**Table 10 Genetic data from the study by De Stefano and Fermenti (1974)**

| Species | Sex | Prov. | DNA +/- s.s. (a.u.) | | |
|---|---|---|---|---|---|
| *P.p. edwardsi* | m | Gabon | 35.67 +/- 0.72 | | |
| | | | | 35.89 +/- 0.81 | |
| *P.p. edwardsi* | f | Gabon | 35.12 +/- 0.83 | | |
| *P. p. potto* | f | Liberia | 35.66 +/- 0.57 | (-) | 35.90 +/- 0.82 |
| *P. p. potto* | m | Liberia | 35.41 +/- 0.73 | | |
| | | | | 35.91 +/- .83 | |
| *P. p. potto* | f | Dahomey | 36.44 +/- 0.77 | | (+) |
| *P. p. potto* | f | Dahomey | 36.12 +/- 0.84 | | |
| *Homo sapiens* | m | | | | 38.12 +/- 0.73 |

It is interesting to note that the values for the two Dahomey specimens are the most distinctive, adding to their appearance of uniqueness. Obviously it would be of great benefit and insight to apply more contemporary and much more powerful tools for genetic analysis to the taxa within *Perodicticus*. While data relevant to the differences within the genus may exist (Roos 2004) it is not published in an accessible fashion in refereed journals.

### 9.5.2. Morphology

While this study does confirm, question, and reveal morphological traits of potential taxonomic relevance, it is clear that further study will help enhance the synthesis with previous taxonomies and will very likely uncover still more unrecognized traits. In addition to a larger sample size a

more detailed and robust morphometric analysis describing features of interest would certainly be a welcome addition to the body of literature on prosimian biology.

### 9.5.3. Development

The pattern of development of different potto groups would be of particular significance in sorting out many questions surrounding the disputed taxa such as *P. p. faustus*. Simply publishing records of observation of the different phases of pelage patterning and coloration would be of great assistance and would cast light on the issue of why some adult specimens tend to resemble sub-adults. Other studies have demonstrated arrested development in primates usually males, based on social and ecological factors (Maggioncalda, Sapolsky and Czekala 2000, Setchell and Dixson 2001). This area of research is greatly lacking for lorisiform primates.

# APPENDIX A

## Specimens of *Perodicticus* Studied

| Museum | Collection Number | Country | Region | Sex | Listed Taxonomy |
|---|---|---|---|---|---|
| AMNH | 269854 | CAR | Dzanga Sanga | male | . |
| AMNH | 269908 | CAR | Dzanga Sanga | female | . |
| AMNH | 269907 | CAR | Dzanga Sanga | female | . |
| AMNH | 184597 | . | . | male | . |
| AMNH | 200232 | . | . | male | . |
| AMNH | 31252 | . | . | . | . |
| AMNH | 54340 | Congo | Swanke | . | *edwardsi* |
| AMNH | 241117 | Cameroon | . | female | *edwardsi* |
| AMNH | 119868 | Fren Eq | . | . | *edwardsi* |
| AMNH | 269909 | CAR | Dzanga Sanga | male | *edwardsi* |
| AMNH | 119864 | Gabon | Kango | female | *edwardsi* |
| AMNH | 119865 | Gabon | Kango | . | *edwardsi* |
| AMNH | 119869 | Fren Eq | . | . | *edwardsi* |
| AMNH | 269917 | CAR | Dzanga Sanga | male | . |
| AMNH | 269851 | CAR | Dzanga Sanga | female | . |
| AMNH | 269860 | CAR | Dzanga Sanga | female | . |
| AMNH | 52682 | Zaire | Akenge | female | *ibeanus* |
| AMNH | 52685 | Zaire | Akenge | male | *ibeanus* |
| AMNH | 52688 | Zaire | Avakubi | female | *ibeanus* |
| AMNH | 52686 | Zaire | Akenge | female | *ibeanus* |
| AMNH | 52691 | Zaire | Medje | female | *ibeanus* |
| AMNH | 52696 | Zaire | Medje | male | *ibeanus* |
| AMNH | 52693 | Zaire | Medje | male | *ibeanus* |
| AMNH | 52692 | Zaire | Medje | female | *ibeanus* |
| AMNH | 52697 | Zaire | Medje | male | *ibeanus* |
| AMNH | 52690 | Zaire | Medje | male | *ibeanus* |
| AMNH | 52702 | Zaire | Medje | male | *ibeanus* |
| AMNH | 52698 | Zaire | Medje | male | *ibeanus* |
| AMNH | 52703 | Zaire | Medje | male | *ibeanus* |
| AMNH | 52700 | Zaire | Medje | female | *ibeanus* |
| AMNH | 52708 | Zaire | Niangara | male | *ibeanus* |
| AMNH | 52707 | Zaire | Medje | male | *ibeanus* |
| AMNH | 52709 | Zaire | Niangara | female | *ibeanus* |
| AMNH | 52710 | Zaire | Niapu | female | *ibeanus* |
| AMNH | 52711 | Zaire | Niapu | female | *ibeanus* |
| AMNH | 52717 | Zaire | Stanleyville | female | *ibeanus* |
| AMNH | 86898 | Zaire | Lukolela | female | *ibeanus* |
| AMNH | 89440 | Liberia | Sawtown | male | *potto* |
| AMNH | 239436 | Liberia | Grand Gedeh | . | *potto* |
| AMNH | 52714 | Zaire | Niapu | female | *ibeanus* |

| | | | | | |
|---|---|---|---|---|---|
| AMNH | 180319 | . | . | . | . |
| AMNH | 52715 | Zaire | Niapu | male | *ibeanus* |
| AMNH | 119066 | Uganda | . | . | *ibeanus* |
| AMNH | 52712 | Zaire | Niapu | female | *ibeanus* |
| AMNH | 52713 | Zaire | Niapu | male | *ibeanus* |
| USNM | 184231 | Kenya | Kumba | male | *ibeanus* |
| USNM | 184232 | Kenya | Lukosa River | male | *ibeanus* |
| USNM | 184227 | Kenya | Kaimosi | male | *ibeanus* |
| USNM | 184230 | Kenya | Kaimosi | female | *ibeanus* |
| USNM | 537770 | Zaire | Tandala | male | *ibeanus* |
| USNM | 439099 | Dahomey | Kpodave | male | *potto* |
| USNM | 439100 | Dahomey | Kpodave | male | *potto* |
| USNM | 439104 | Dahomey | Kpodave | female | *potto* |
| USNM | 439096 | Dahomey | Kpodave | female | *potto* |
| USNM | 438102 | Dahomey | Kpodave | female | *potto* |
| USNM | 282371 | Ghana | Oda | . | *potto* |
| USNM | 414398 | Ghana | Legon | male | *potto* |
| USNM | 429533 | Ghana | Oda | male | *potto* |
| USNM | 429535 | Ghana | Oda | male | *potto* |
| USNM | 429534 | Ghana | Oda | female | *potto* |
| USNM | 429536 | Ghana | Oda | female | *potto* |
| USNM | 465906 | Ghana | Adamso | female | . |
| USNM | 465908 | Ghana | Oda | male | . |
| USNM | 465907 | Ghana | Oda | male | *potto* |
| USNM | 465909 | Ghana | Oda | male | . |
| USNM | 465910 | Ghana | Oda | female | *potto* |
| USNM | 414399 | Ghana | Ahiriso | female | *potto* |
| USNM | 414400 | Ghana | Ahiriso | male | *potto* |
| USNM | 465912 | Ghana | Adamso | male | *potto* |
| USNM | 450055 | Ivory Coast | Jacqueville | male | *potto* |
| USNM | 450058 | Ivory Coast | Yapo Sud | male | *potto* |
| USNM | 450056 | Ivory Coast | Jacqueville | female | *potto* |
| USNM | 450057 | Ivory Coast | Ehania | male | *potto* |
| USNM | 450050 | Ivory Coast | Blekoum | female | *potto* |
| USNM | 450051 | Ivory Coast | Jacqueville | male | *potto* |
| USNM | 450052 | Ivory Coast | Jacqueville | male | *potto* |
| USNM | 450053 | Ivory Coast | Ehania | female | *potto* |
| USNM | 450054 | Ivory Coast | Jacqueville | female | *potto* |
| USNM | 465895 | Ivory Coast | Kahin | male | *potto* |
| USNM | 465894 | Ivory Coast | Diali | female | *potto* |

| | | | | | |
|---|---|---|---|---|---|
| USNM | 465893 | Ivory Coast | Diali | female | *potto* |
| USNM | 465892 | Ivory Coast | Diali | female | *potto* |
| USNM | 465900 | Ivory Coast | Guitri | female | *potto* |
| USNM | 465899 | Ivory Coast | Kahin | male | *potto* |
| USNM | 465898 | Ivory Coast | Diali | female | *potto* |
| USNM | 465897 | Ivory Coast | Diali | female | *potto* |
| USNM | 465902 | Ivory Coast | Yabrasso | male | *potto* |
| USNM | 465903 | Ivory Coast | Guitri | male | *potto* |
| USNM | 465904 | Ivory Coast | Guitri | female | *potto* |
| USNM | 465901 | Ivory Coast | Guitri | female | *potto* |
| USNM | 253619 | Liberia | Monrovia | female | *potto* |
| USNM | 270156 | Liberia | Belli Yella | male | *potto* |
| USNM | 270530 | Liberia | Belli Yella | . | *potto* |
| USNM | 481737 | Liberia | Grand Gedeh | female | . |
| USNM | 481738 | Liberia | Grand Gedeh | male | *potto* |
| USNM | 481739 | Liberia | Grand Gedeh | female | *potto* |
| USNM | 181740 | Liberia | Grand Gedeh | male | . |
| USNM | 481744 | Liberia | Grand Gedeh | female | *potto* |
| USNM | 481741 | Liberia | Grand Gedeh | male | *potto* |
| USNM | 377270 | Nigeria | Ashaka | male | *potto* |
| USNM | 377271 | Nigeria | Ashaka | female | *potto* |
| USNM | 377272 | Nigeria | Asaba | male | *potto* |
| USNM | 377273 | Nigeria | Calabar | male | *potto* |
| USNM | 379619 | Nigeria | Sapoba | male | *potto* |
| USNM | 300793 | . | . | male | . |
| USNM | 303034 | . | . | . | . |
| USNM | 320056 | . | . | . | . |
| USNM | 536964 | . | . | female | . |
| USNM | 536965 | . | . | male | . |
| CM | 4557 | Cameroon | Lolodorf | male | *edwardsi* |
| CM | 3895 | Cameroon | Elat | female | *edwardsi* |
| CM | 41117 | Cameroon | Eskeka | female | *edwardsi* |
| CM | 3913 | Cameroon | Lolodorf | male | *edwardsi* |
| CM | 3926 | Cameroon | Lolodorf | female | *edwardsi* |
| CM | 4628 | Cameroon | Lolodorf | male | *edwardsi* |
| CM | 13187 | Cameroon | Melan | male | *edwardsi* |
| CM | 16085 | Cameroon | Lolodorf | male | *edwardsi* |
| CM | 16087 | Cameroon | Lolodorf | male | *edwardsi* |
| CM | 16186 | Ivory Coast | Toumodi | male | *potto* |
| CM | 4663 | Cameroon | Metet | male | *edwardsi* |

| | | | | | |
|---|---|---|---|---|---|
| CM | 42330 | Cameroon | Ebolowa | male | *edwardsi* |
| CM | 5100 | Cameroon | Metet | male | *edwardsi* |
| CM | 10321 | Cameroon | Sangmelima | male | *edwardsi* |
| CM | 10322 | Cameroon | Sangmelima | male | *edwardsi* |
| CM | 57887 | Uganda | Kayonza Forest | male | *ibeanus* |
| CM | 57886 | Kenya | Kakamega Forest | male | *ibeanus* |
| CM | 57885 | Kenya | Kakamega Forest | female | *ibeanus* |
| CM | 69182 | Ivory Coast | Lakota | male | *potto* |
| CM | 69183 | Ivory Coast | Lakota | male | *potto* |
| CM | 69184 | Ivory Coast | Lakota | female | *potto* |
| CM | 69185 | Ivory Coast | Toumodi | male | *potto* |
| CM | 16086 | Cameroon | Lolodorf | male | *edwardsi* |

# APPENDIX B

## Additional Taxa Examined

| Museum | Number | Sex | Genus | Species | Subspecies | Country | Locale |
|---|---|---|---|---|---|---|---|
| USNM | 256739 | male | *Loris* | *tardigradius* | *tardigradius* | Sri Lanka | Nikeweratiya |
| USNM | 114692 | female | *Loris* | *tardigradius* | *tardigradius* | . | . |
| USNM | 256737 | female | *Loris* | *tardigradius* | *tardigradius* | Sri Lanka | Nikeweratiya |
| USNM | 241488 | male | *Nycticebus* | *coucang* | *bengalensis* | Thailand | . |
| USNM | 355064 | male | *Nycticebus* | *coucang* | *bengalensis* | Thailand | Chiengmai |
| USNM | 296915 | female | *Nycticebus* | *coucang* | *bengalensis* | Thailand | Kanchanaburi |
| USNM | 260593 | male | *Nycticebus* | *coucang* | *bengalensis* | Thailand | Chiengmai |
| USNM | 296916 | male | *Nycticebus* | *coucang* | *bengalensis* | Thailand | Lampang |
| USNM | 258870 | female | *Nycticebus* | *coucang* | *bengalensis* | Thailand | Chanthaguri |
| USNM | 296513 | male | *Nycticebus* | *coucang* | *bengalensis* | Thailand | Kanchanaburi |
| USNM | 296914 | female | *Nycticebus* | *coucang* | *bengalensis* | Thailand | Kanchanaburi |
| USNM | 300015 | male | *Nycticebus* | *coucang* | *bengalensis* | Thailand | . |
| USNM | 300016 | male | *Nycticebus* | *coucang* | *bengalensis* | Thailand | . |
| USNM | 535153 | male | *Nycticebus* | *coucang* | *bengalensis* | Thailand | Ubol |
| USNM | 142232 | male | *Nycticebus* | *coucang* | *borneanus* | Indonesia | Borneo |
| USNM | 300014 | female | *Nycticebus* | *coucang* | *bengalensis* | Thailand | . |
| USNM | 307712 | male | *Nycticebus* | *coucang* | *bengalensis* | Thailand | Nakhon Panom |
| USNM | 307713 | female | *Nycticebus* | *coucang* | *bengalensis* | Thailand | Loei |
| USNM | 317187 | female | *Nycticebus* | *coucang* | *borneanus* | Malaysia | Sabah |
| USNM | 198857 | female | *Nycticebus* | *coucang* | *borneanus* | Indonesia | Borneo |
| USNM | 198267 | male | *Nycticebus* | *coucang* | *borneanus* | Indonesia | Borneo |
| USNM | 142239 | female | *Nycticebus* | *coucang* | *borneanus* | Indonesia | Borneo |
| USNM | 142237 | male | *Nycticebus* | *coucang* | *borneanus* | Indonesia | Borneo |
| USNM | 142238 | female | *Nycticebus* | *coucang* | *borneanus* | Indonesia | Borneo |
| USNM | 142236 | male | *Nycticebus* | *coucang* | *borneanus* | Indonesia | Borneo |
| USNM | 142233 | male | *Nycticebus* | *coucang* | *borneanus* | Indonesia | Borneo |
| USNM | 317198 | male | *Nycticebus* | *coucang* | *borneanus* | Malaysia | Sabah |
| USNM | 292553 | male | *Nycticebus* | *coucang* | *borneanus* | Malaysia | Sabah |
| USNM | 292554 | female | *Nycticebus* | *coucang* | *borneanus* | Malaysia | Sabah |
| USNM | 142235 | male | *Nycticebus* | *coucang* | *borneanus* | Indonesia | Borneo |
| USNM | 105022 | female | *Nycticebus* | *coucang* | *coucang* | Malaysia | Trengganu |
| USNM | 114151 | male | *Nycticebus* | *coucang* | *coucang* | Malaysia | Johore |
| USNM | 290462 | male | *Nycticebus* | *coucang* | *coucang* | Malaysia | Selangor |
| USNM | 291274 | female | *Nycticebus* | *coucang* | *coucang* | Malaysia | Selangor |
| USNM | 291275 | . | *Nycticebus* | *coucang* | *coucang* | Malaysia | Selangor |
| USNM | 115496 | female | *Nycticebus* | *coucang* | *coucang* | Malaysia | Pahang |
| USNM | 355347 | female | *Nycticebus* | *coucang* | *coucang* | Malaysia | Selangor |
| USNM | 843849 | female | *Nycticebus* | *coucang* | *coucang* | Malaysia | Perak |
| USNM | 294414 | male | *Nycticebus* | *coucang* | *coucang* | Malaysia | Selangor |
| USNM | 355065 | male | *Nycticebus* | *coucang* | *coucang* | Thailand | Nakhon Sritamraj |
| USNM | 283915 | female | *Nycticebus* | *coucang* | *coucang* | Malaysia | . |

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| USNM | 291732 | . | *Nycticebus* | *coucang* | *coucang* | Malaysia | . |
| USNM | 300000 | male | *Nycticebus* | *coucang* | *coucang* | Malaysia | Selangor |
| USNM | 488075 | male | *Nycticebus* | *coucang* | *coucang* | Malaysia | Pahang |
| USNM | 488076 | female | *Nycticebus* | *coucang* | *coucang* | Malaysia | Perak |
| USNM | 488078 | male | *Nycticebus* | *coucang* | *coucang* | Malaysia | Selangor |
| USNM | 488079 | female | *Nycticebus* | *coucang* | *coucang* | Malaysia | Selangor |
| USNM | 488080 | male | *Nycticebus* | *coucang* | *coucang* | Malaysia | Trengganu |
| USNM | 355065 | male | *Nycticebus* | *coucang* | *coucang* | Thailand | Nakhon Sritamraj |
| USNM | 141141 | female | *Nycticebus* | *coucang* | *hilleri* | Indonesia | Sumatra |
| USNM | 114450 | male | *Nycticebus* | *coucang* | *hilleri* | Indonesia | Sumatra |
| USNM | 267400 | female | *Nycticebus* | *coucang* | *hilleri* | Indonesia | Sumatra |
| USNM | 270595 | male | *Nycticebus* | *coucang* | *hilleri* | Indonesia | Sumatra |
| USNM | 271186 | male | *Nycticebus* | *coucang* | *hilleri* | Indonesia | Sumatra |
| USNM | 521835 | male | *Nycticebus* | *coucang* | *javanicus* | Indonesia | West Java |
| USNM | 521836 | male | *Nycticebus* | *coucang* | *javanicus* | Indonesia | West Java |
| USNM | 258234 | male | *Nycticebus* | *pygmaeus* | . | Vietnam | Blad Donai |
| USNM | 256913 | . | *Nycticebus* | *pygmaeus* | . | Vietnam | Bien Hoa |
| USNM | 377275 | male | *Arctocebus* | *calabarensis* | *calabarensis* | Nigeria | Calabar |
| USNM | 511930 | male | *Arctocebus* | *calabarensis* | *calabarensis* | Cameroon | Kumba |
| USNM | 377274 | female | *Arctocebus* | *calabarensis* | *calabarensis* | Nigeria | Calabar |
| USNM | 365729 | female | *Galago* | *crassicaudatus* | *lonnbergi* | Mozambique | Manica/Sofala |
| USNM | 365730 | male | *Galago* | *crassicaudatus* | *lonnbergi* | Mozambique | Manica/Sofala |
| USNM | 365731 | female | *Galago* | *crassicaudatus* | *lonnbergi* | Mozambique | Manica/Sofala |
| USNM | 365728 | male | *Galago* | *crassicaudatus* | *lonnbergi* | Mozambique | Manica/Sofala |
| USNM | 365727 | male | *Galago* | *crassicaudatus* | *lonnbergi* | Mozambique | Manica/Sofala |
| USNM | 365725 | female | *Galago* | *crassicaudatus* | *lonnbergi* | Mozambique | Manica/Sofala |
| USNM | 365732 | male | *Galago* | *crassicaudatus* | *lonnbergi* | Mozambique | Manica/Sofala |
| USNM | 365733 | male | *Galago* | *crassicaudatus* | *lonnbergi* | Mozambique | Manica/Sofala |
| USNM | 365735 | female | *Galago* | *crassicaudatus* | *lonnbergi* | Mozambique | Manica/Sofala |
| USNM | 425415 | male | *Galago* | *crassicaudatus* | *lonnbergi* | Rhodesia | Manicaland |
| USNM | 425414 | female | *Galago* | *crassicaudatus* | *lonnbergi* | Rhodesia | Manicaland |
| USNM | 425413 | male | *Galago* | *crassicaudatus* | *lonnbergi* | Rhodesia | Mashonaland |
| USNM | 368616 | female | *Galago* | *crassicaudatus* | *lonnbergi* | Rhodesia | Beatrice |
| USNM | 397672 | male | *Galago* | *crassicaudatus* | *panganiensis* | Kenya | Taveta |
| USNM | 398075 | female | *Galago* | *crassicaudatus* | *panganiensis* | Kenya | Taveta |
| USNM | 35093 | female | *Galago* | *crassicaudatus* | *panganiensis* | Kenya | Arusha Wa-Cini |
| USNM | 336287 | male | *Galago* | *crassicaudatus* | *panganiensis* | Kenya | Taveta |
| USNM | 35091 | male | *Galago* | *crassicaudatus* | *panganiensis* | Kenya | Taveta |
| USNM | 184200 | male | *Galago* | *crassicaudatus* | *panganiensis* | Kenya | Ndi |
| USNM | 184198 | male | *Galago* | *crassicaudatus* | *panganiensis* | Kenya | Ndi |
| USNM | 396164 | male | *Galago* | *crassicaudatus* | *panganiensis* | Kenya | . |
| USNM | 397618 | male | *Galago* | *crassicaudatus* | *panganiensis* | . | . |
| USNM | 397318 | male | *Galago* | *crassicaudatus* | *panganiensis* | . | . |
| USNM | 397725 | female | *Galago* | *crassicaudatus* | *panganiensis* | . | . |
| USNM | 398043 | male | *Galago* | *crassicaudatus* | *panganiensis* | . | . |
| USNM | 435018 | male | *Galago* | *demidovii* | *pusillus* | Ghana | Efeipo Krom |
| USNM | 435016 | male | *Galago* | *demidovii* | *pusillus* | Ghana | Efeipo Krom |
| USNM | 421550 | male | *Galago* | *demidovii* | *pusillus* | Dahomey | Eastern Region |
| USNM | 421549 | male | *Galago* | *demidovii* | *pusillus* | Dahomey | Eastern Region |

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| USNM | 412721 | male | *Galago* | *demidovii* | *pusillus* | Ghana | Eastern Region |
| USNM | 414401 | male | *Galago* | *demidovii* | *pusillus* | Ghana | Ashanti Region |
| USNM | 414404 | male | *Galago* | *demidovii* | *pusillus* | Ghana | Ashanti Region |
| USNM | 414403 | male | *Galago* | *demidovii* | *pusillus* | Ghana | Ashanti Region |
| USNM | 412723 | male | *Galago* | *demidovii* | *pusillus* | Ghana | Eastern Region |
| USNM | 414402 | female | *Galago* | *demidovii* | *pusillus* | Ghana | Ashanti Region |
| USNM | 412722 | female | *Galago* | *demidovii* | *pusillus* | Ghana | Eastern Region |
| USNM | 125435 | male | *Galago* | *demidovii* | *pusillus* | Cameroon | Bulu Country |
| USNM | 450061 | male | *Galago* | *demidovii* | *ssp* | Ivory Coast | Ethania |
| USNM | 450060 | male | *Galago* | *demidovii* | *ssp* | Ivory Coast | Blekoum |
| USNM | 465825 | male | *Galago* | *demidovii* | *ssp* | Ivory Coast | Diali |
| USNM | 437917 | male | *Galago* | *demidovii* | *ssp* | Togo | Agou |
| USNM | 437918 | female | *Galago* | *demidovii* | *ssp* | Togo | Ezime |
| USNM | 437919 | male | *Galago* | *demidovii* | *ssp* | Togo | Ezime |
| USNM | 84533 | female | *Galago* | *elegantulus* | *elegantulus* | Guinea | Rio Muni |
| USNM | 86427 | . | *Galago* | *elegantulus* | *elegantulus* | Gabon | Como River |
| USNM | 184210 | female | *Galago* | *senegalensis* | *braccatus* | Kenya | Ndi |
| USNM | 184211 | female | *Galago* | *senegalensis* | *braccatus* | Kenya | Ndi |
| USNM | 184212 | male | *Galago* | *senegalensis* | *braccatus* | Kenya | Ndi |
| USNM | 184207 | . | *Galago* | *senegalensis* | *albipes* | . | . |
| USNM | 184209 | . | *Galago* | *senegalensis* | *albipes* | . | . |
| USNM | 465848 | . | *Galago* | *senegalensis* | *senegalensis* | . | . |
| USNM | 465849 | . | *Galago* | *senegalensis* | *senegalensis* | . | . |
| USNM | 465854 | . | *Galago* | *senegalensis* | *senegalensis* | . | . |
| USNM | 465850 | . | *Galago* | *senegalensis* | *senegalensis* | . | . |
| USNM | 184204 | . | *Galago* | *senegalensis* | *sotikae* | . | . |
| USNM | 84206 | . | *Galago* | *senegalensis* | *sotikae* | . | . |
| USNM | 251625 | . | *Galago* | *senegalensis* | *zanzibaricus* | . | . |
| USNM | 184218 | . | *Galago* | *senegalensis* | *zanzibaricus* | . | . |
| USNM | 184219 | . | *Galago* | *senegalensis* | *zanzibaricus* | . | . |
| USNM | 184220 | . | *Galago* | *senegalensis* | *zanzibaricus* | . | . |
| USNM | 184208 | . | *Galago* | *senegalensis* | *albipes* | . | . |
| USNM | 352253 | female | *Galago* | *senegalensis* | *granti* | Mozambique | Massangena |
| USNM | 352254 | male | *Galago* | *senegalensis* | *granti* | Mozambique | Massangena |
| USNM | 376864 | female | *Galago* | *senegalensis* | *moholi* | Botswana | Tsau |
| USNM | 382704 | female | *Galago* | *senegalensis* | *moholi* | Botswana | Gaberones |
| USNM | 425405 | male | *Galago* | *senegalensis* | *moholi* | Botswana | Tsodilo Hills |
| USNM | 367851 | male | *Galago* | *senegalensis* | *moholi* | Botswana | Joverega |
| USNM | 382706 | male | *Galago* | *senegalensis* | *moholi* | Botswana | Chukutsa |
| USNM | 83390 | . | *Galago* | *alleni* | . | Gabon | Librevlle |
| USNM | 377278 | female | *Galago* | *alleni* | . | Nigeria | Oban |
| USNM | 352254 | male | *Galago* | *alleni* | . | Mozambique | Massangena |
| USNM | 365714 | . | *Galago* | *crassicaudatus* | *crassicaudatus* | . | . |
| USNM | 365715 | . | *Galago* | *crassicaudatus* | *crassicaudatus* | . | . |
| USNM | 365311 | . | *Galago* | *crassicaudatus* | *crassicaudatus* | . | . |
| USNM | 197181 | . | *Galago* | *crassicaudatus* | *garnetti* | . | . |
| USNM | 197182 | . | *Galago* | *crassicaudatus* | *garnetti* | . | . |
| USNM | 197183 | . | *Galago* | *crassicaudatus* | *garnetti* | . | . |
| USNM | 197814 | . | *Galago* | *crassicaudatus* | *garnetti* | . | . |
| USNM | 35092 | . | *Galago* | *crassicaudatus* | *lasiotis* | . | . |

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|---|---|---|---|---|---|---|---|
| USNM | 184199 | . | *Galago* | *crassicaudatus* | *lasiotis* | . | . |
| USNM | 184202 | . | *Galago* | *crassicaudatus* | *lasiotis* | . | . |
| USNM | 184196 | . | *Galago* | *crassicaudatus* | *kikuyensis* | . | . |
| USNM | 184197 | . | *Galago* | *crassicaudatus* | *kikuyensis* | . | . |
| USNM | 254710 | male | *Galago* | *crassicaudatus* | *agisynbanus* | Tanzania | Zanzibar |

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